FISHERIES RESEARCH BOARD OF CANADA

Biological Station, St. Andrews, N.B.
1908-1958

Fifty Years of Research in Aquatic Biology

By J. L. Hart, *Director*

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BEGINNINGS

In 1908 a continuing base for research in marine biology was established at St. Andrews, N.B. This auspicious step was taken by a group of men called The Board of Directors. On the urging of a group of scientists of the Royal Society of Canada, the Minister of Marine and Fisheries set up this board in 1898 as The Board of Management of the Marine Biological Station of Canada. Members of the Board included: Professor E. E. Prince, Commissioner of Fisheries, Chairman; Professors D. P. Penhallow (Secretary-Treasurer) and E. W. MacBride, both of McGill University; Professors R. Ramsay Wright and A. B. Macallum, University of Toronto; Professor L. W. Bailey, University of New Brunswick; Professor A. P. Knight, Queen's University; The Reverend V. A. Huard, Laval University; and Dr. A. H. MacKay, representing Dalhousie University. These men and their colleagues in the Royal Society of Canada and the British Association for the Advancement of Science admirably combined vision with

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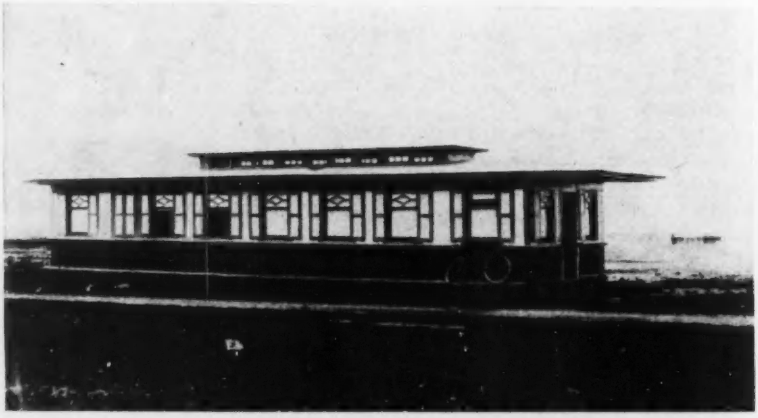
caution. In the economy of 1958 the decision of 1908 to establish a small centre for marine research may seem trivial, or obvious. It was not so in 1908, when Canada's mere seven million people were spread over some three and a half million square miles and the total annual value of Canadian fisheries was only thirty million dollars. The record shows that the decisions to recommend national participation in marine biological research was reached only after most careful consideration. Similar careful thought was given to the later decision to locate an Atlantic station at St. Andrews.



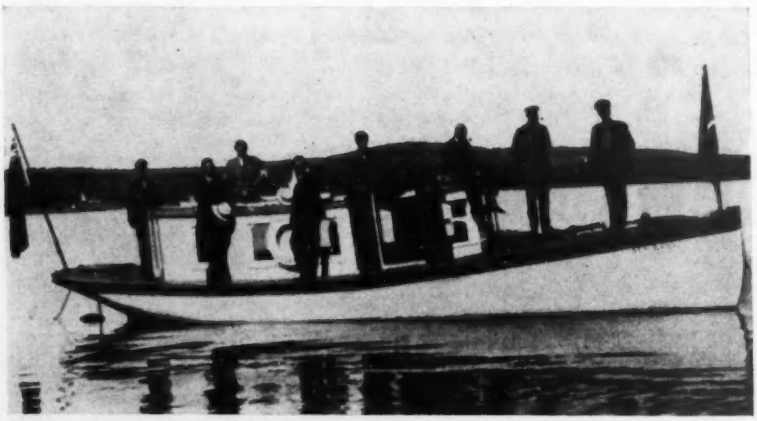
Canada's first biological station (movable, on a scow) at Indian Point, St. Andrews, N.B., 1899. The Station was built in 1899, and operated as follows: at St. Andrews, 1899–1900; Canso, N.S., 1901–1902; Malpeque, P.E.I., 1903–1904; and Gaspé, P.Q., 1905–1906. The scow foundered while being moved to Seven Islands, P.Q., in 1907; it was beached at Grande Vallée, P.Q., and later dismantled.

Early Work in Marine Biology

Some research in marine biology had been carried out on the Canadian Atlantic coast prior to 1908. Amateur and professional investigators, notably Professor W. F. Ganong of the University of New Brunswick, had studied independently and alone. More-organized research was authorized in 1898 when approval was given to construct a portable laboratory as a base for experienced investigators in marine research. This laboratory was completed in time to accommodate active research in 1899.

"The building has been described as resembling a pullman car externally and is placed upon a scow so that it can be towed from one location to another. Its total length is 50 feet and the main laboratory is 30 feet by 15 feet in breadth and it is provided with shelving, tables, porcelain basins, and salt-water and freshwater supplies. A small library apartment, and other rooms, afford storage accommodation. A small good working library has been collected, including the magnificent "Challenger" reports presented by the British Government through the Right Honorable Joseph Chamberlain, and a considerable series of valuable papers and reference works."

The portable laboratory was used for two years at each of the following places: St. Andrews, N.B., 1899 and 1900; Canso, N.S., 1901 and 1902; Malpeque, P.E.I., 1903 and 1904; Gaspé, P.Q., 1905 and 1906. While the scow carrying the laboratory was being towed from Gaspé to its next location at Seven Islands, P.Q., in 1907, it sprung a leak and was beached at Grand Vallée, P.Q. There it was placed under the administration of the St. Andrews Station and was ultimately abandoned.



The *Sea Gull*, 1908–15.

Name of the Station

Early in its history, the St. Andrews Station became appropriately known as the Atlantic Biological Station. When Newfoundland became part of Canada, the long-established Government Laboratory in St. John's and the Atlantic Biological Station came under the same Canadian administrative unit. As both were on the Atlantic, the old name was no longer suitable. The Station is now known officially as Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.

ARRANGEMENTS FOR RESEARCH

Provisions for carrying out scientific work have been modified through the years to meet changing conditions and to grow with the times. From 1908 until 1912, under the Board of Directors, and from then until 1924, under the Biological Board of Canada, scientists did not remain at the Station throughout the year. Research was done by qualified scientists from Canadian universities who carried their researches forward during the summers in exchange for bare living and travelling expenses. Much of the research was done by Board members, who remained practising scientists while developing a policy for the Station. Dr. A. P. Knight was particularly active. During this period, the Station was administered by a seasonal resident director with the assistance of a curator.

Evidently from the first, the Station "kept prominently before it in all its work the benefit of the fisheries while carrying out in a thoroughly satisfactory and scientific way its seasonal investigations". This conforms with the directive contained in the Biological Board Act of 1912 and subsequent revisions which states in part, "The Board . . . has the conduct and control of investigations of practical and economic problems connected with marine and freshwater fisheries, flora, and fauna, and such other work as may be assigned to it by the Minister".

The Atlantic Biological Station, Brandy Cove, St. Andrews, N.B., in 1909.
Left to right: the water tower, main laboratory, residence, fish handling shop and carpenter shop. Photograph taken from the St. Croix River.

After the first year of operating the shore-based station, the Resident Director, D. P. Penhallow, strongly recommended the appointment of a full-time scientific curator. In 1916, A. G. Huntsman, Curator since 1911, became the first full-time or permanent scientific staff member. A second full-time scientist was added in 1924 in the person of A. H. Leim. For a few years, the scientific staff spent the winters at the Department of Biology at the University of Toronto. Year-round scientific work at St. Andrews began in 1928 when H. B. Hachey stayed at the Station through the winter of 1928–29. Until 1934 volunteer seasonal workers and permanent staff members worked together in profitable harmony. In that year the permanent scientific staff was nine in number and Canada was in the depths of a stubborn economic depression. Appropriations were inadequate to support both kinds of work and the arrangements for using volunteer scientists were suspended. Although visiting scientists have worked gratis on special projects for short periods in later years, the full use of volunteer investigators has never been restored.

An increasing demand for practical results made the appointment of a permanent staff necessary, since volunteers could not undertake the specific

investigations demanded and devote the necessary time to them. This was recognized administratively in 1937 when the Biological Board of Canada became the Fisheries Research Board of Canada, with the implied changes in primary responsibilities. The trend toward research applicable to increasing the yields from the fisheries was emphasized during the war years, 1940 to 1945, with the objective of providing increasing amounts of protein food.

The post-war period has been one of continuing growth for the Station. Basically the growth has stemmed from the increasing realization of the administrative need for thorough objective investigation of the fisheries and the stocks of fish and invertebrates which support them. Some of the needs have been emphasized by the Canadian necessity to meet research commitments under international fisheries agreements. The growth of the scientific staff is shown below in a statement of permanent scientific staff size at three-year intervals: 1924, 2; 1927, 2; 1930, 6; 1933, 11; 1936, 9; 1939, 9; 1942, 9; 1945, 10; 1948, 12; 1951, 23; 1954, 24; 1957, 29.

GENERAL BIOLOGICAL RESEARCH TO 1934

The destiny of a research organization depends upon its tasks and the people carrying them out. Research objectives of the biological station at St. Andrews have been varied. This was inevitable from the broad scope of fishery problems and the wide geographical area covered.

Investigators at the Station in 1919.
Front row: Professors C. J. Connolly, J. W. Mavor and A. G. Huntsman.
Middle row: Miss E. Shanly, Professor E. E. Prince, Professor A. Vachon.
Back row: Dr. L. Gross, Miss B. K. Mossop, Miss Rose Prince, Miss J. MacFarlane.

Early researches from the portable laboratory studied the food of local commercial fishes, the weir fishery, and the life history of clams and the fishery they support. A study of the fauna was begun as well as an investigation of the development of the eggs and larvae of pelagic fishes. Even before the beginning of shore-based work, chemical studies were commenced on the composition of medusae and the effects of pollution.

The *Edward E. Prince*, 1913–32; shown just after its launching.

From 1908 to 1911 much emphasis was given to studies of the fauna and flora of the area. Attention was given to life-history studies, to physiology, to such practical matters as keeping qualities of squid, and to bait studies. It is interesting to note that in 1909 the Curator of the Station spent considerable time studying oyster spat and larvae in Prince Edward Island; in fact, he was the first to identify larvae of the American oyster in the plankton. Attention was also being given to the effects of lath spacing on the release of lobsters from traps, and the hydrography of Kennebecasis Lake and the Passamaquoddy area were subjects of investigation. These are all problems which still command attention at the Station.

Following 1912, under the Biological Board of Canada, work continued in widely diversified fields to provide information on many aspects of fish and fisheries. Basic to the other work, then and since, were studies of the marine fauna and flora of the region. These studies did not stop at recording and describing the species present. The life histories of selected forms were subjected to careful investigation with special attention given to the food relations among the various species and to the incidence and development of larval fishes. An interesting phase in work in biochemistry was the study of the occurrence of insulin in fishes. Various aspects of behaviour were studied. In this field, as in others, the work was extended to include freshwater forms.

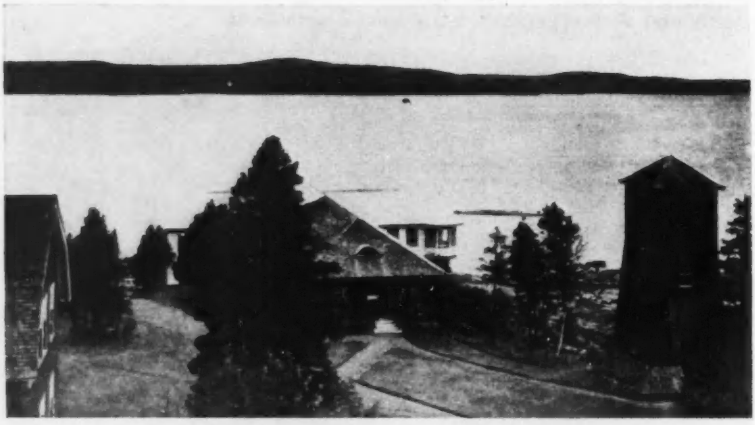
HYDROGRAPHY, SURVEYS, AND EXPEDITIONS, 1912 TO 1934

From its earliest days, the scientists associated with the Station's work were concerned with the ways in which the physical and chemical conditions of the water and the ocean currents controlled the distribution of various species of fish. Oceanography has, accordingly, always been an important part of the Station's work. General observations of water temperatures and densities were begun in 1913. They were continued throughout the years with increasing regularity and with organization for special objectives.

Captain A. E. Calder, Master and Collector, 1909–1950.

The Station was the focus of several surveys and expeditions to other parts of the Canadian Atlantic coast. For the most part, these were combined operations involving both biological and hydrographic work. The first was the *Canadian Fisheries Expedition, 1914–15.* This expedition, under the distinguished leadership of Dr. Johan Hjort, sought accurate knowledge of the fish and hydrography of Canadian Atlantic waters which could be aid in exploiting the fisheries resource, and in particular it sought the solution of certain urgent problems concerning the herring stocks of the Gulf of St. Lawrence and the outer coast of Nova Scotia. The research was broadly planned and included physical oceanography, studies on plankton of all kinds, including the eggs and larvae of many

commercial species of fish, and the detailed biology of the herring. An important part of the results was the conclusion that at least four quite distinct groups of herring are to be found in the area. They were: (1) the Newfoundland type which grows slowly during its first year and rapidly later, (2) the southern Gulf of St. Lawrence type which grows rapidly during its first year and slows down with increasing age, (3) the Cape Breton type with moderate first year growth



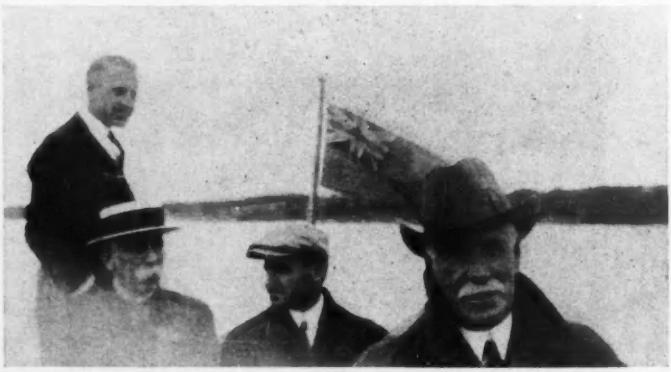
The Atlantic Biological Station, in 1923.
Left to right: residence, main laboratory and water tower. In the distance the Maine shore of Passamaquoddy Bay.

and rapid growth from the third summer on, and (4) the southwestern Nova Scotia type which grows well throughout its life span. The work of the Expedition provided the first critical assessment of oceanographic conditions in the general area and directed attention to the puzzling and all important problems related to the supply of commercial fish in the region.

In 1917, to meet the need for further knowledge of the undeveloped fishery resources in the Gulf of St. Lawrence region, an expedition to the southeastern Gulf was based on Eastern Harbour, near Cheticamp, Cape Breton. The survey lasted from May until September and for the most part dealt with the area between the base and the Magdalen Islands. Hydrographic records were kept for association with the extensive biological collections.

In the following year, 1918, the Board selected the Miramichi River and Bay as an area for special study in the Gulf of St. Lawrence region. The base was at Loggieville. The work was started early in May and carried through to the end of August. It involved investigations of the varied conditions not only seaward about 30 miles into the Gulf but also inland to the head of tide at Redbank on the Northwest Miramichi River. As in the previous surveys, hydrographic observations were emphasized and temperature records and water

samples were taken regularly. A wide variety of gear was used for biological collections. In considering the collections, special attention was given to herring, smelt, alewife, tomcod, striped bass, and the algae. As a primary object of the investigation was to obtain knowledge for increasing food by use of the fishery resource, experiments on the effectiveness of various kinds of bait were also undertaken.



Members and scientists of the Biological Board at St. Andrews in 1924. *From the left*: Mr. A. H. Leim, Professor E. E. Prince, Professor A. G. Huntsman, Professor A. P. Knight.

In 1916 hydrographic and biological surveys were made of St. Mary Bay, Annapolis Basin, and Yarmouth Harbour, N.S., and Kennebecasis Bay, N.B. Some of these minor surveys were repeated in later years.

The North American Council on Fishery Investigations, set up in 1920 to determine the extent to which co-operation in investigations in international fisheries was desirable, held its first meeting in 1921 and met regularly thereafter to and including 1938. The Director of the Station was a member of the Council which had representation from Canada, the United States of America, Newfoundland, and France. It provided a very useful forum for the exchange of results and ideas. It played a part in developing the thinking in several of the major investigations and was partly instrumental in establishing stations for the systematic recording of sea-water temperatures.

During the years 1922 to 1930, on the initiation of the North American Council on Fishery Investigations, ocean currents off the Canadian Atlantic coast were investigated by an intensive series of drift bottle experiments. These extensive experiments showed much about both local and off-shore surface currents and provide the background for all subsequent work.

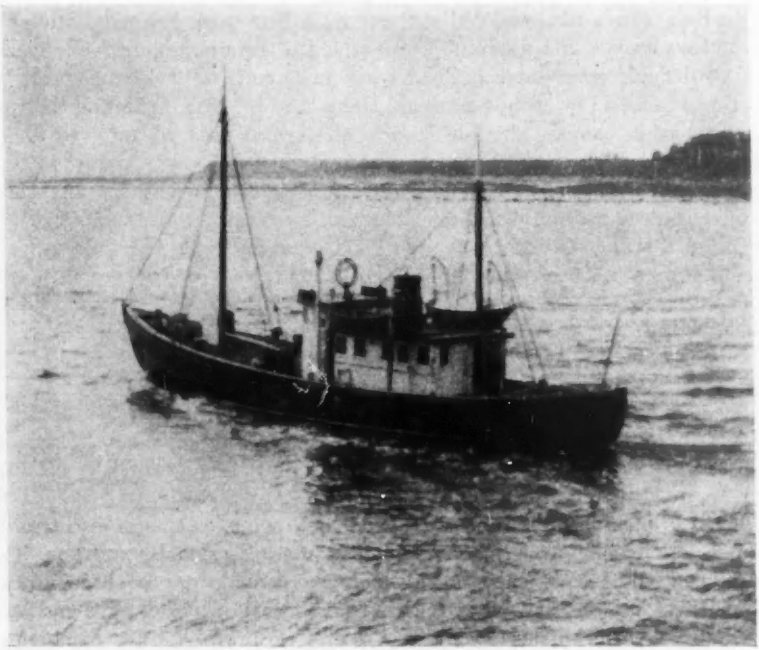
An expedition to the Strait of Belle Isle in 1923 was also stimulated by the North American Council. Two Canadian vessels were involved, the Station's own boat, the *Edward E. Prince*, remaining in the area from July until the middle of September. Sections across the Labrador Current were studied and its course

The residence building, 1923.

was followed by means of drift bottles. The general survey included the region from Cabot Strait and Anticosti Island through the Strait of Belle Isle and around the eastern and southern coast of Newfoundland. The movement of cod and their abundance or scarcity at the important fishing grounds at Blanc Sablon, on the north shore, and the Quirpon region of Newfoundland were found to be related to the temperatures produced by the mixing of Gulf water and cold water from the Labrador Current in the Strait of Belle Isle.

In 1924 and 1925 a series of surveys was made of parts of the coast to assess the extent of warm water suitable for the growth of young lobsters. Five parties covered the following areas: Shippegan to Charlot, N.B.; Dartmouth to Jeddore, N.S.; Halifax to Canso, N.S.; Boutilier to Port Medway, N.S.; Shelburne to Argyle, N.S.

During the summer of 1930 a well-equipped and well-manned steam trawler was sent to Hudson Bay by the Fisheries Department under H. B. Hachey of the Biological Station to make fishing trials in the open part of the Bay. In the same year a land party investigated the fisheries of the Churchill River. The results showed unequivocally that there is no off-shore stock of commercial fish in the area. Small catches of usable fish were taken in the rivers but it was shown beyond doubt that commercial fishing in the rivers could not prove profitable. The conclusions of this thorough examination confirmed those reached by more cursory examinations made under the Board's auspices in 1920, 1927, 1928, and 1929.



The *Zoarces*, 1931–40.

Through its Assistant Director, the Station contributed in 1930 to the work of the International Fact Finding Commission for Lake Champlain with a study of the food of yellow perch there.

In 1931 the International Passamaquoddy Fisheries Commission was formed by Canada and the United States of America to investigate the probable effects on local fisheries of damming Passamaquoddy and Cobscook Bays in a project to develop hydro-electric power from the tides. Six highly competent special scientists were engaged for research in biology and hydrography. They reported in 1933, that the herring fishery in Passamaquoddy Bay would probably be reduced to negligible proportions, that herring weirs outside the dams would probably be affected but in unpredictable ways, and that there was little prospect of effects along the coast of Maine or even serious effects at Grand Manan.

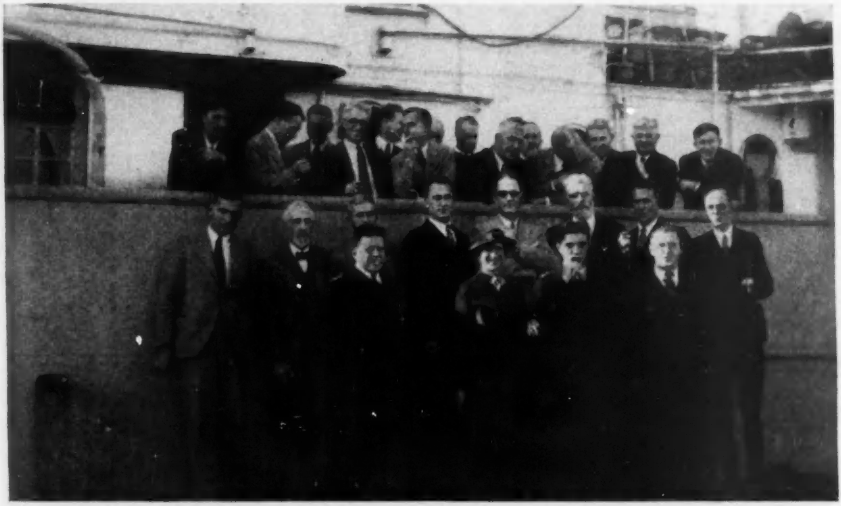
RESEARCH IN FOOD TECHNOLOGY, 1912 TO 1934

During this period, much research effort at the St. Andrews laboratory was directed toward studies of the food value of fish and of proper handling methods. With the establishment of the Biological Board's technological station in Halifax in 1925, most of the work in this field was diverted there. However, some of the seasonal investigators continued to deal with problems bearing on handling as

long as they were accommodated at the Station. The work covered a wide range of problems, species and disciplines, and engaged the attention of many workers. Some of the important subjects dealt with concerned: the bacteriology of fresh and frozen fish, and of canned sardines, clams, and lobsters, including the causes of swollen cans; canning dogfish; studies of the processes of autolysis and decomposition; the protein and other constituents of fish muscle; digestion of fish flesh; the principles of smoking and the causes for reddening in salt fish; the effects of heat on fish muscle; the histology of freezing; the desirability of quick freezing of fish fillets and the saleability of the product; the bacteriology of fish slime; the importance of sanitation in vessel holds.

LOBSTERS

Because of its commercial value and its biological interest, the lobster has attracted the attention of the Station's investigators from early days. From 1910 to 1913, experiments were conducted to determine the effects of lath spacing in releasing undersized lobsters. In 1913 and the following year, interest was broadened to include life-history studies on such points as conditions for proper hatching and development, mating, potential rearing grounds, and age. There were few, if any, years when no advances were made on the life history of lobsters. Investigations showed extremely heavy losses of lobster eggs and larvae in attempts at artificial rearing and led to the closure of lobster hatcheries in 1917. Studies on the technology of lobster canning began in 1917 and continued into the twenties. Through the early thirties major contributions to our knowledge of the life history were made. Tagging methods were developed and used. Studies on growth and berried lobsters were pursued. These in turn led to work on moulting, the breeding cycle, and maturity. On several occasions, the conditions affecting the survival of the young pelagic larvae were investigated. With the appointment in 1937 of a full-time investigator, increasing attention was given to the effects on the lobster populations of the intensity of fishing and of regulation. New tagging methods were used to determine the fraction of the population taken by the fishery. Information on natural mortality and growth rates were applied to framing recommendations for regulation. Extensive sampling at representative fishing ports has followed the effects of regulation so that in effect research and regulation became a combined tool to assure the best use of the resource. In 1943 the idea of lath spacing was revived and by 1946 extensive experiments had shown that a high proportion of undersized lobsters were released from traps with properly spaced laths. Lath spacing, accordingly, seemed practical as a conservation measure and was put into effect, but had to be dropped because of the opposition of fishermen in a few areas. In 1948 regular surveys of larval abundance were begun in Northumberland Strait. They show the numbers of small lobsters that settle to be relatively independent of the breeding stock. With other observations, these surveys will be useful in predicting catches.



Respite from meetings of the North American Council on Fishery Investigations at the French research vessel *Président Théodore Tissier*, Halifax, N.S., Sept. 19–21, 1934.
Front row: Ed. LeDanois, Mrs. A. B. Needler, P. Desbrosses, V. D. Vladykov.
Second row: A. W. H. Needler, J. P. McMurrich, A. G. Huntsman, C. E. Jackson, E. Higgins, M. L. Beaugé, C. Iselin, H. F. S. Paisley.
Third row: E. Priol, W. C. Herrington, S. A. Beatty, H. Thompson, A. E. Calder, H. B. Bigelow. W. A. Found, G. Belloc, H. B. Hachey.
Fourth row: R. J. Bean, D. H. Sutherland, D. B. Finn (partly hidden), A. H. Leim, O. E. Sette.

Lobsters are peculiar among fisheries products in that many are marketed alive. Studies were started in 1949 to determine the conditions under which they will survive. Much study has been given to the tolerable limits of temperature, oxygen content, and salinity of the water and the interaction among them so that now the Station is able to give expert advice to professional handlers. This work has had many ramifications. Studies during 1957 included work on suitable conditions for air holding as an aid in providing light weight packing for air shipment.

Conventional wooden lobster traps are light in water, offer considerable surface to the sea, and are accordingly subject to loss or damage by storm action. A strong metal trap could be relatively light in air and heavy in water while offering less surface to surge on the bottom. Exploration of the possibility of using metal traps began in 1953. The work to date has shown that metal traps suffer little damage from severe storms but during cold-water periods do not catch lobsters as effectively as wooden traps. The principles affecting the usefulness of metal traps continue to attract research attention and the Station is providing consultation service for practical tests carried out by the Development Service of the Department of Fisheries.

Aerial view of the surroundings of the Sub-station at Ellerslie, P.E.I. At the right, an arm of Malpeque Bay. The Station building and dock are on the point in the foreground. Photograph taken in 1941.

OYSTERS

The biology and culture of Maritime oysters has attracted the attention of marine biologists from the beginning of the century. In 1903, when the floating laboratory was stationed at Malpeque, P.E.I., food, reproduction, and local varieties were studied as well as practical problems dealing with cultch to catch larvae.

From 1914 to 1925, few interrupted studies were carried on in Prince Edward Island. In 1916 a devastating disease wiped out the Malpeque oyster stocks and the rule-of-thumb oyster culture that was carried on there. Early investigations dealt with the causes of the failure in production, with growth and food, and with the effects of salinity, light, crowding, and of type of bottom. Surveys of oyster grounds were made along the New Brunswick shore where the disease did not occur, as far north as Caraquet.

In 1929 the Research Board's oyster work was intensified with the establishment of a permanent sub-station of the St. Andrews Station at Ellerslie, P.E.I., and with the appointment of full-time investigator to direct it. The aim was to establish oyster culture on a sound scientific basis. The investigator was also responsible for directing Fisheries Department work in oyster culture and for

administering leases. This dual responsibility for research and application was maintained until 1948 when responsibility for departmental work was assumed by a new appointee. Research activities have always been carried out in the closest co-ordination with the Department and industry. Early basic research studied the hydrographic, meteorological and other conditions affecting spawning, sex reversal, spatfall and spat survival and growth. Practical results of the work were the development of a method of floating artificial cultch for mass collection of spat, a system of accurate prediction of spatfall, and the use of floating trays for rearing young oysters. Tests of dykes for rearing young oysters on intertidal flats were begun a little later and are still regarded as hopeful. Other work included investigations of the food and life history of the larvae and the fatness and condition of adult oysters. Surveys of oyster grounds in New Brunswick and Nova Scotia were carried out to assess the possibilities for culture. Methods of restricting damage by shipworms to gear used in oyster culture and by starfish to the oysters themselves were developed and the efficiency of growing oysters in brackish water inlets were explored.

In 1931 studies of the fatal oyster disease which spread from Malpeque Bay and wiped out all susceptible stock in other areas was resumed. Thereafter the important features of the epidemiology were discovered and methods of study were developed which have since been used in investigating recent outbreaks of the disease along the Gulf of St. Lawrence shores of New Brunswick and Nova Scotia.

In order to make research results more readily available to the industry, experimental oyster farms in addition to the one in Malpeque Bay were established by the Department of Fisheries. One of these at Shediac, N.B., was closed but those established at Gillis Cove in Bras d'Or Lake, N.S., 1936, at Malagash, N.S., 1937, and Shippegan, N.B., 1942, still provide very effective testing bases for the Station's experimental findings and are useful demonstration centres.

Two secondary investigations have been brought to a close recently. The boring sponge which weakens the shells of oysters and thus makes them hard to store and hard to open was thoroughly studied from 1952 to 1957. Saturated brine dips are now recognized as a satisfactory control measure. Work done in 1952 and 1953 found ways of controlling eel grass which is a pest in oyster grounds but the methods are too costly for general use. Much of the work of the last 25 years has been directed to developing an economic method of growing bedding oysters (c. 1½ in.) from spat. Tray rearing which was practical for many years is now too expensive. There now seems to be good hope of using at least one natural inlet where water and bottom conditions favour growth and survival of young oysters but inhibit starfish, their principal enemy.

CLAMS

Several species of clam have been investigated from time to time from the Station. In 1899 and 1900 the life history and the fishery of soft-shelled clams was studied. In 1914 supposed diseases of quahaugs were investigated and in

the following years the growth and other aspects of the biology of soft-shelled clams were reported on. During this period also, some work was done on the life history of the mussel.

From 1930 until the present with the exception of three years in the mid-thirties, some work was carried out on clams each year. Early work on soft-shelled clams concentrated on natural enemies, growth, and productivity. In the early forties attention was directed to small slow growing clams and the possibility of allowing these to be used at small sizes or of moving them to faster growing ground. Thorough consideration was given to the possibility of clam farming to relieve the growing scarcity of clams but by 1948 it was realized that ordinarily such operations could not be economically profitable. As early as 1944 attention was directed to conventional hand digging methods which are inefficient and wasteful. From 1951 on, thinking moved toward the idea of a mechanized clam digger. This proposal became a practical reality in 1955 and was perfected mechanically by 1957. Its biological effects on soft-shelled clams remain to be tested.

Work on bar clams and quahaugs has been less regular. The general life history of the quahaugs was fairly well worked out by 1939. Growth is generally slow and is related to position on the beach, being best just below low tide. Water flow is important for growth but other factors tested seem unimportant. The role of the large clam drill *Polynices* as an enemy was confirmed by 1940.

In contrast to the quahaug the bar clam was shown by 1943 to grow quickly. It should stand exploitation well. Careful surveys led to the conclusion in 1948 that there are not many populations dense enough to sustain profitable dredging operations for this rather deep species. However, the recently developed mechanized digger promises to open new stocks of both quahaugs and bar clams to exploitation.

Two other species of animal have been studied in relation with the clam work. The green crab is a serious predator of soft-shelled clams and made its appearance in southern Maritime waters in 1951. It became very abundant by 1954 and is now declining. It no doubt contributed to the recent serious decline in clam populations. The other species is the European oyster. Its requirements were studied from the point of view of introducing it to augment failing supplies of clams. A trial planting was made in 1957 with reasonable success.

SCALLOPS

Scallop research from St. Andrews was begun in 1927 by an examination of scallop beds at L'Etang Harbour and off Digby in the Bay of Fundy and continued in 1932 with studies of growth rates in various places around the Maritimes. By 1936 the studies covered food for adults, maturity, spawning, the physical requirements for egg development, drift of larvae, varying success of year-classes, and the possible effects of the increasing commercial fishery. Most of these studies were suspended in 1936 following the drowning of the investigator-in-charge, Mr. J. A. Stevenson, while on duty at Digby, N.S., which was then the centre of the Maritimes scallop fishery.

From 1937 until 1941 some work was done on the Digby grounds with fine drags to estimate future recruitment but work was dropped during the war years, 1942 to 1946.

In 1947 studies of growth rate and recruitment in the Digby area were renewed. These data and information on fishing mortality were used for prediction and for management recommendations. By 1948 it was realized that

Mr. H. C. White, Biologist, 1927–55.

scallops were being used at an uneconomically small size. During the next few years a great deal of effort went into developing a practical fishing gear which would spare small scallops to grow further. In 1952 a workable savings gear with large mesh in the drags was worked out and has been required by regulation since 1953. In 1951 a successful method of long range prediction of landings, based on hydrographic records and known survival conditions for young scallops, was developed for the Digby area. In 1954 an attempt to refine it by censusing potential recruits was explored but the increased accuracy of prediction did not justify the extra effort involved.

Recurring devastating mass mortalities of Gulf of St. Lawrence scallop populations have been a continuing barrier to the development of a stable fishery in that region. Field and laboratory studies of temperature tolerances of scallops indicate that the mortalities are caused by flooding the beds by

warm water in late summer. On the basis of this discovery the ring-size regulation applied to the Digby fishery in 1954 was not applied in the Gulf. Consequently harvesting of scallops is permitted there by small-mesh drags as soon as the animals reach commercially useful sizes.

Since 1949 considerable effort has gone into exploration for new fishing grounds. These efforts have had several minor successes and one important one in 1953 and 1954 with the discovery of extensive productive fishing grounds on St. Pierre Bank.

HERRING

Herring were the subject of occasional study during the early years of work at St. Andrews. From 1929 to 1936 studies were made on parasites, the hydrographic and other factors controlling catches, the relationship between food availability and feeding and fatness. Behaviour studies showed that different sizes of herring behave differently.

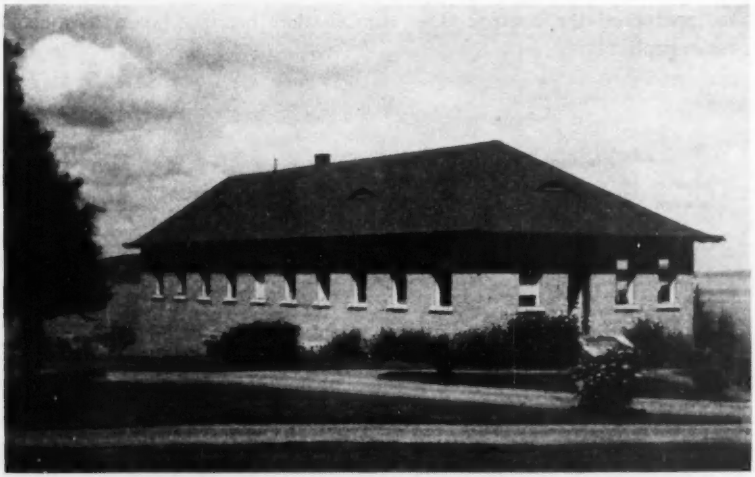
After a break of several years an investigation was begun in 1942 which indicated and confirmed that winter seining had no deleterious effect on total production in the area. In 1943 a search was begun for knowledge to use in increasing the fishery. The indication that herring is a great unused resource led to the formation in 1944 of the Atlantic Herring Investigation Committee. This committee included representatives of the Governments of Canada, Newfoundland, New Brunswick, Nova Scotia, Prince Edward Island, and Quebec. It sought to find ways of expanding both the volume of the catch and variety in the use of herring. Work under the Committee based at St. Andrews carried out extensive explorations for herring in the Gulf of St. Lawrence and adjacent Newfoundland and Nova Scotia areas with echo sounders, gill nets, bottom trawls, and pelagic trawls. Biological studies of herring covered length and age analyses, vertebral counts, and spawning habits, and hydrographic research increased knowledge of water character and transport in the area. In all a firm basis was established for further work. From 1950 to 1953 exploratory fishing was continued under the Fisheries Research Board with midwater trawls, bottom trawls, and gill nets in the Gulf of St. Lawrence and off the Nova Scotia coasts. Fishing tests were supported by population studies. These explorations indicated the feasibility of commercial drift-netting in some areas. In 1953 exploratory fishing was again extended into Newfoundland waters.

During the years 1954 to 1956 additional work involved food, larval distribution, and studies of an epidemic disease caused by fungus parasites.

In 1956 the Station became responsible for Canadian research to meet the needs of the International Passamaquoddy Fisheries Board. This Board is assigned the task of forecasting the effects on fisheries in the region of placing dams across the entrance to Passamaquoddy Bay to develop electric power. This assignment is to be completed in October of 1959. It calls for an intensive examination of the present situation, and of the behaviour and requirements of the fish species involved.

TROUT

The Station's research on trout is closely connected with studies of fish culture and limnology. During much of its early history, the Station was involved in studies of hatchery mortalities and to a less extent in considering the suitability of lakes for planting hatchery stock. In 1923 pioneer work on the fates of trout fry planted under various conditions was begun. Attention was given to various

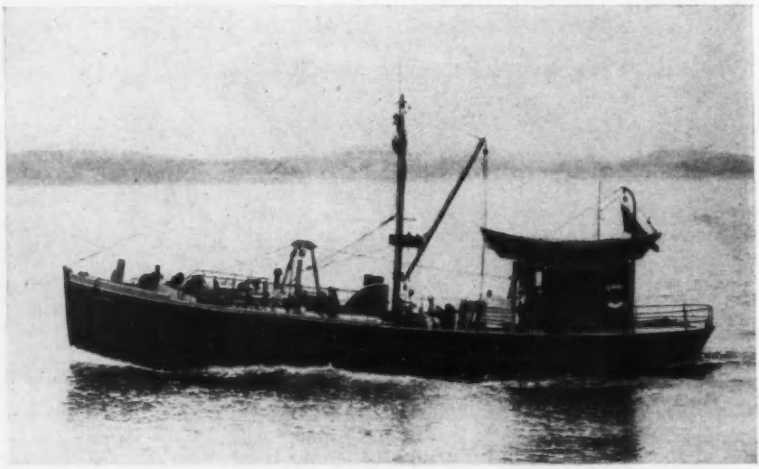


The main laboratory, as rebuilt after the fire of 1932. Photograph taken in 1935.

aspects of the life history and nutrition of young trout, such as food, the factors controlling successful hatching, the effects of diet of adult fish on egg production, the food of competitor fishes, etc. In 1930 an experimental hatchery and six experimental ponds were built at St. Andrews. The ponds were used for a series of experiments to determine the effects of adding different amounts of fertilizer on their capacities to support trout foods and trout. This method of improving production seemed effective when carried out with restraint. Another series of experiments began in 1932 tried the effects of increasing production of trout by flooding meadows so as to take advantage of the cycle produced by the decay of the killed-out organic matter on the ground. However, it was impractical to keep temperatures down and oxygen up in most flooded areas fed only by surface drainage. Thorough limnological surveys of soft-water lakes in Charlotte County showed them to be unproductive of trout foods and trout. Returns from stocking were very poor. Poisoning enemy and competitor fish with copper sulphate or derris root and restocking were found to present practical difficulties in stratified lakes and gave results commensurate with the productive capacity of the water.

Observations made over the first 15 years of study seemed to indicate the need for experimentation on altering natural conditions to improve trout production and utilization and for turning attention to the biological needs of different areas. Sucessful tests in applying these attitudes have been made in Prince

Edward Island and in Charlotte County of New Brunswick. In Prince Edward Island where conditions for trout propagation and growth are good, pond formation on streams has increased trout utilization by anglers and thus increasing availability. This was begun in 1943. There seems to be no biological deterrents to this form of management and run-arounds to facilitate the investigation of sea-run individuals gave promising results in 1956. In Crecy Lake, N.B., applying the principles in 1943 led to successive use of stocking with hatchery fish, fertilization, and predator control. The combination has produced a spectacular increase in production.



The *J. J. Cowie*, 1943–58 (still in use).

SALMON

The first recorded interest in salmon at the St. Andrews Station was in 1913 when the Chairman of the Board led in the experimental development of a new type of fish pass for carrying salmon over the falls in the Magaguadavic River. This experiment involved the progressive concept of an automatic elevator to lift the fish over the obstruction.

The years from 1931 to 1937 were devoted to a variety of studies. An important phase of the work was the study of life history of salmon from different localities and at different stages by examining the relationship between scale pattern and environmental conditions. The scale work was supplemented by behaviour observations. Natural stocks were compared with hatchery plantings and the food of young salmon stages were compared with those of competitors. Analyses were made of catch data to 1931. Tests of the tendency of salmon to return to their native river gave positive indications but trials of the inheritability of the early running habit from 1934 to 1936 produced negative results.

In the years from 1935 to 1947 most of the Board's salmon research for the Maritime Provinces was carried out separately under the guidance of Dr. A. G. Huntsman. During this period there were successive focal points for principal effort. The relation of commerical fisheries to angling, conditions governing entrance of salmon into the river, and relationships of bird predators on young salmon were studied on the Margaree River (1934 to 1938). An experiment on the effects of controlling water discharge for getting early river ascent was

Captain E. G. Rigby (*left*), Master and Curator, 1916–19 and 1921–51; with Dr. A. W. H. Needler (*right*), Director, 1941–54. Photograph taken on the occasion of Captain Rigby's retirement in 1951.

performed on the Moser River (1939 to 1945). Studies of factors associated with optimum production of seaward migrating smolts were initiated on the Petitcodiac in 1941 and are still going on. From 1946 to 1953 special studies on behaviour of salmon, and on principles concerned with use were conducted in the Shubenacadie, Grand Lake area. During the course of the work many aspects of the salmon's life history and management were examined. Some of the more important dealt with: The effects on salmon stocks of predation by predatory birds and other enemies. The use of hatchery stock under various conditions. Where are salmon in the sea? Homing. The effects of water temperatures on angling. The effectiveness of artificial freshets and of stream obstructions on the availability of salmon in streams. The usefulness of size limits. Food. The behaviour of smolts

and adults in relation to current, and of parr in relation to temperature, cover, and light. In general, it was concluded that the most effective management would be by working through nature rather than by attempting directly to control salmon populations. These researches grew from work at the Station, their data and lessons were incorporated into the work which followed.

In 1949 a Federal–Provincial Co-ordinating Committee on Atlantic Salmon was set up to consider a policy for administering the salmon resource. The research program necessary to provide the basis for action was proposed by a Scientific Sub-Committee. The Station served a key role in co-ordinating research effort and in carrying out the research program in the Atlantic provinces.

In 1947 a second and more complete study of the effectiveness of controlling fish-eating birds for increasing salmon smolt production was begun on the Pollett River (Petitcodiac system). Control here increased smolt production by more than four times. In 1950 it was put into effect on an experimental basis on the Northwest Miramichi, where similar improvements in parr survival were observed. A larger scale trial on the whole Miramichi watershed was embarked upon later but the results are being obscured by the effects of DDT spraying. Electrofishing using direct current was found useful and from 1950 on was progressively incorporated into censusing techniques. From 1950 total annual smolt productions in the Miramichi system were estimated by marking migrating smolts and calculating from the proportion of marked individuals taken in samples of known size further down the river. Smolt marking in various rivers also provided information in 1952 and subsequently on the utilization of salmon from various rivers in the sea. Careful examination of the effectiveness of stocking practice was continued, especially on the Pollet River and has recently produced valuable indications on the amount of spawn for best production, the proper spacing of plantings, and the proper size of salmon for planting. The number of adults needed to provide adequate natural seeding has also been explored.

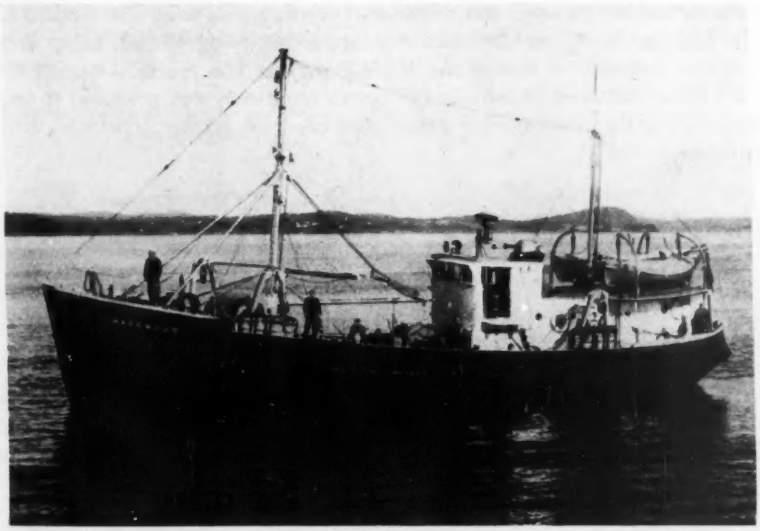
Since 1954 the salmon investigation has given much attention to the effects on salmon and on the aquatic insects on which salmon feed of spraying watersheds with DDT to control spruce budworm outbreaks. A high proportion of young salmon in the rivers are killed and the aquatic insect fauna is first drastically reduced and later much altered. However, spraying seems necessary. Attention in 1957 and 1958 is accordingly being directed to exploring remedial and mitigating action.

GROUNDFISH

Work on the groundfish started in 1914 with growth studies on cod and hake and general life-history studies of haddock. In the ensuing years a life-history study of the haddock was carried out and general studies were extended to include pollock, flounder, plaice, cunner, tomcod, dogfish, etc. In 1931 a survey of the fisheries of the Fundy area was begun and provided impetus for organizing additional research effort. In the 10 years following 1931, the general life history of cod and haddock was explored including growth, distribution, migrations,

temperature preferences, spawning and egg distribution and the fisheries and their statistics. Accordingly, when the investigation was suspended in 1941, because of restricted resources and the transfer of the research vessel *Zoarces* in 1940 for wartime use, the inshore cod and haddock populations were defined.

In 1942 the wartime and longer term need for new fishing methods was recognized and in succeeding years a variety of new fishing gears and fisheries were brought into production on the Atlantic coast. Longlining, inshore draggers, Danish seining, Norwegian jigger were all promoted by the Station and all have



The *Harengus*, 1946–58 (still in use).

contributed substantially to the financial well-being of the Maritimes. Power dories were developed in an effort to mechanize line fishing from off-shore schooners. Tests with other gear, such as sunken gill nets, did not provide promise that they would be economically successful.

By 1945 the competitive and conservation aspects of the international groundfish fishery were realized. With this in mind a thorough general study was initiated. An early step was to define the existing conditions by sampling the sizes and ages of fish in commercial catches and by arranging to have fishing skippers supply log book records of their operations. Short-term studies of halibut and of yellowtail and winter flounders were carried out.

In 1945 a life-history study of the nematode parasite which depreciates the quality of fillets was started and a study of the marine mammals initiated in 1948 contributed information about the alternate host of the parasite. Studies of parasite incidence and of the seal hosts were continued actively until 1956 when the

mammal investigation was transferred to the Board's Arctic Unit in Montreal and parasite work was taken over by the Insitute of Parasitology.

In 1949 the International Commission for the Northwest Atlantic Fisheries was formed to make possible the best utilization of fisheries resources in its area. The Commission provided a strong impetus to intensified work by the scientists of the 10 participating nations. Effort was continued on statistics of the fishery, definitions of populations and their movements, and growth rates, and was extended to include natural and fishing mortality rates and the effectiveness of various kinds of gear in catching or releasing fish of different sizes. Initial emphasis was on haddock but cod and redfish and other species were also studied intensively. The results led in 1953 to a regulation specifying 4½-inch mesh in trawl nets in the southern section of the ICNAF region. The practical results of this test are being followed closely. In 1957 mesh regulation was extended to include waters around the Maritime Provinces. The need for further restriction is being investigated.

OCEANOGRAPHY

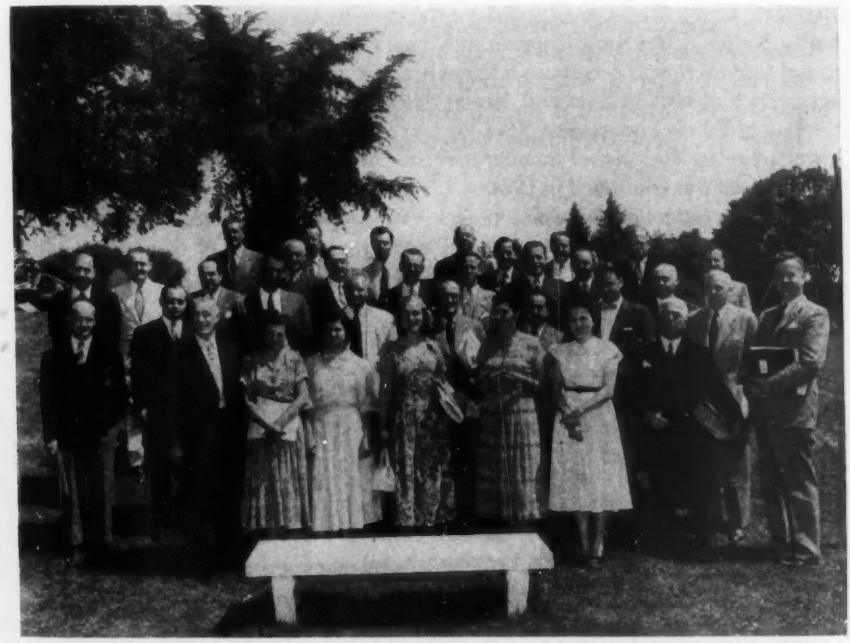
The study of the currents and the contents of the water in which fish move and grow has been part of the Station's work from the outset. In practically every year some phase of the hydrography of the region has been studied. From the important pioneer work of the Canadian Fisheries Expedition, 1914–1915 to the present, various aspects of the floating animals and plants in the water have been studied also. In earlier investigations these studies were qualitative or descriptive. Recent work has been planned to answer specific questions about the distribution and availability of larval fishes or fish food.

Every day since 1921 the water temperature at the St. Andrews Biological Station wharf has been taken. The accumulated data comprise an unique and valuable record of seasonal and cyclic changes.

From 1931 to 1939, the conditions off the Scotian Shelf were followed in a series of cruises and the results analysed. They demonstrated three main movements, (1) a southwest movement along the coast, (2) an anti-clockwise circulation in the southern part of the Shelf, and (3) a complicated vortex over the extreme southwestern portion of the Shelf. For the surface layers the winter transport of water exceeds that of summer.

From 1940 to 1946 suitable vessels for oceanographic research were taken over by the Navy and no research was carried out. In 1946 the Joint Committee on Oceanography was set up with representatives of the Fisheries Research Board, the Naval Service, and the National Research Council. Later representatives from other interested branches have been added. Dr. H. B. Hachey, who later became Chief Oceanographer for Canada, was secretary for this group and was stationed at the St. Andrews Station where he guided the activities of the Atlantic Oceanographic Group. Throughout he has arranged for close co-operation with fisheries groups and with oceanographic research agencies in the United States.

The work of the Atlantic Oceanographic Group has been directed toward defining the major water masses off our coast and to study of their detail and variation. Surveys have dealt with such areas as (1) the Gulf of St. Lawrence and the Newfoundland area with special attention to the freshwater economy of the Magdalen Shallows, the Gaspé Current, the effects of flow through the Strait of Canso, the flow through Cabot Strait, and winter studies with the *Labrador* to discover the source of the cold water intermediate layer, (2) the Gulf Stream, (3) the Scotian Shelf, partly in an attempt to explain the unusually warm water conditions prevailing there during the years around 1951, (4) the Bay of Fundy and its connecting waters, (5) the warm saline band of water, called slope water, between coastal waters and the Gulf Stream, and (6) variations in water transport.



Participants in the second annual meeting of the International Commission for the Northwest Atlantic Fisheries, held at St. Andrews June 30 to July 9, 1952.

Front group: J. Côté, H. F. Barbier (France), J. H. MacKichan, Miss D. Inkpen, Miss E. Sullivan, Miss J. Welsh, A. T. A. Dobson (U.K.), Miss N. Parker, V. Trelles (Spain), Mrs. S. Cunningham, Commander T. de Almeida (Portugal), A. V. Tåning (Denmark), W. R. Martin.

Rear group: L. A. Walford (U.S.A.), H. Graham (U.S.A.), C. Ojeda (Spain), R. Gushue, F. W. Sargent (U.S.A.), L. Thygesen (Denmark), J. Lamb, P. D. Espada (Spain), J. L. Kask, S. Bates, B. Rasmussen (Norway), B. Dinesen (Denmark), O. Lund (Norway), C. E. Lucas (U.K.), G. Rollefsen (Norway), W. C. Herrington (U.S.A.), R. S. Wimpenny (U.K.), E. Jacobsen (Denmark), A. W. H. Needler, P. Hansen (Denmark), F. D. McCracken.

The Station is the headquarters for research in the oceanography of the Eastern Canadian Arctic. The Atlantic Oceanographic Group manned the oceanographic research aboard the *Labrador* when in 1954 she circumnavigated the continent in a single year, and from 1955 to 1957 provided the research teams for oceanographic studies of the Arctic.

OTHER INVESTIGATIONS

Wood Borers

In 1923 the Station's facilities were used to commence a survey to determine the extent of damage to piling and other wooden structures by wood borers in relation to hydrographic conditions. This work was financed by the National Research Council of Canada and undertaken in co-operation with the United States National Research Council and the Department of Public Works. It was found that there was a definite relation between hydrographic conditions and the occurrence of both gribble and teredo. High salinity and low temperature as in the Bay of Fundy and eastern Nova Scotia favours the gribble, whereas somewhat lower salinities and higher summer temperatures favour the teredo. The work on wood borers was continued in 1924.

The investigation of wood borers was reopened in 1935 and continued through 1939. It was done primarily to assess the possibility of damage to piling

Dr. A. G. Huntsman (*second from left*), Curator and Director of the St. Andrews Station 1911–1933, with Dr. G. B. Reed (*second from right*) and Professor J. R. Dymond (*left*), Chairman and Vice-Chairman respectively of the Fisheries Research Board of Canada, and Dr. Stewart Bates (*right*), Deputy Minister of Fisheries for Canada, on the occasion of Dr. Huntsman's retirement from the Board in 1953.

in Saint John Harbour and also to learn more about methods of controlling the pests in equipment used in oyster culture.

Shad

In 1919 a thorough study of the shad in the Maritimes was begun with special emphasis on conditions in the Shubenacadie River and Minas Basin, N.S. A full scientific report was published in 1924 covering the spawning, the development and factors affecting this, the food of the larvae and of the older stages, the growth throughout life, and an analysis of the fishery and the reasons for its vicissitudes.

Baitworms

In 1950 explorations for baitworms were begun in an effort to develop an additional source of income for clam diggers. Stocks of two kinds of worms were discovered of which the so-called bloodworm is much the more important. By 1954 these worms were producing more than $35,000 annually. Studies showed substantial unused parts of the stock and high fecundity. It was concluded, accordingly, that regulation of the fishery was unnecessary and study was dropped.

Seals

In 1949 an investigation of seals off the Canadian Atlantic coast was begun. This investigation had two objectives. (1) The local harbour and grey seals had been found to carry one stage of a parasite which deteriorates cod fillets and the feasibility and desirability of controlling the parasite by controlling the host was to be studied. (2) The Arctic harp and hooded seals are heavily exploited animals of commerce. One objective was to explore the desirability of conservation measures for them. A great deal of information was collected about the life histories of the local species. One interesting finding was that the grey seal which had formerly been regarded as a biological rarity is quite a common animal. Aerial surveys to census the harp seal population on the ice floes were begun and will be repeated at intervals to detect changes in the abundance in the herds. In 1955 all marine mammal work was transferred to the Board's Arctic Unit in Montreal.

Smelts

The smelt was the object of intermittent investigation during the early days of the Station. In 1920 and 1922 seasonal investigators studied its life history. It was not, however, until 1942 that a systematic study of the species was begun, centred on the Miramichi River. This investigation, which closed in 1957, made a thorough study of the fishery and of the life history and behaviour of the fish. The work has led to recommendations for closing the tidal reaches of certain rivers, for increasing the mesh size in nets to spare small fish, for stream clearance to spread out the spawning areas, and for lengthening the fishing season.

Irish Moss

Of the many thousands of tons of seaweed around the coast of the Maritime Provinces, Irish Moss is the only one with an established industrial market. A survey of this resource and its processing methods and markets was made in 1941. From 1943 to 1951 studies were modified to include curing methods and improving quality. In 1954 biological studies were resumed on the ecology of Irish Moss and false Irish Moss and on the growth, reproduction, and regeneration after harvesting.

Public Health and Shellfish

Shellfish and especially clams can be unfit for food for two kinds of reasons. As they are handled fresh and eaten raw or lightly cooked, those from sewage-polluted areas are dangerous to public health unless they are cleansed. Since 1940 the Station has worked in close co-operation with the Department of National Health and Welfare and the Department of Fisheries in developing cleansing methods for oysters, clams, and quahaugs. These protect public health while allowing full use of the resource.

Clams and mussels in the Fundy region are sometimes quite dangerous in another way. They eat a poisonous (to man) minute plant with impunity but accumulate the toxin. People eating the shellfish are made quite ill with paralytic shellfish poisoning and sometimes die. From 1943 until 1949, the Station's investigations discovered the plant that carries the poison, studied the occurrence of poisonings, and assisted the Department of National Health and Welfare in establishing measures to protect the public. In 1957 an epidemic of poisonings, mostly among people who disregarded warning signs, revived interest in this work and provided further opportunity for clinical observations.

PROVIDING INFORMATION

The results of the Station's researches are made known to the scientific world through the various publications of the Fisheries Research Board and its predecessors, and through numerous specialized journals of scientific societies and other agencies. The Board's journals and bulletins have been:

Contributions to Canadian Biology, 1902 to 1925.
Contributions to Canadian Biology and Fisheries, 1926 to 1934.
Journal of the Biological Board of Canada, 1934 to 1937.
Journal of the Fisheries Research Board of Canada, 1938 to the present.
Bulletins of the Biological Board of Canada, 1918 to 1937.
Bulletins of the Fisheries Research Board of Canada, 1938 to the present.

Many of the Bulletin series are semi-popular handbooks, based on various aspects of the work done.

Non-technical accounts of various researches appear in *Progress Reports of the Atlantic Coast Stations* which have appeared about every half year since 1931.

To meet special needs, general or technical circulars have been prepared from time to time in the following series:

Circulars, General Series, of the Biological Station, St. Andrews, N.B.;
Circulars, Statistical Series, of the Biological Station, St. Andrews, N.B.;
Circulars, Oyster Farming Series, of the Biological Station, St. Andrews, N.B.

Considerable information on the general biology of fishes has been made available through the *Fisheries Fact Sheets* and in *Trade News*, both published by the Department of Fisheries.

In addition to using the various channels for printed information mentioned above, the Station has regularly supplied the Department of Fisheries, the Fishing Industry, and the public with information pertaining to regulation or application by reports, memoranda, courses of instruction, and consultation.

PEOPLE AT THE STATION

The work of a research organization depends upon the scientists involved, their direction, and the kind of assistance they receive from the technical staff. Accordingly this account would not be complete without mention of the directors, the productive scientists, and outstanding lay staff.

Directors

Dr. D. P. Penhallow was the first "Resident Director" of the Station. He was on the committee responsible for choosing the site. He was ably assisted by his curator, Dr. J. Stafford, who in 1907 examined alternate sites which led to the choice of St. Andrews. It was he and Dr. Stafford who bore the brunt of the inevitable difficulties attached to clearing the land and constructing the original buildings in 1908. Dr. Penhallow suffered from ill health during the last two years of his office and died in 1910.

Dr. A. G. Huntsman was at first Curator and later Director of the Station, from 1911 until 1933. He brought will, energy and broad knowledge to bear on many of the problems of the Canadian Atlantic coasts and his original outlook did much to set the Station's pattern of thought. From 1935 until his retirement from the Board's employment in 1953 he took a productive interest in salmon research.

Dr. A. H. Leim was Director of the Station during the difficult years of recovery from the economic depression of the 1930's. He was Director from 1934 until 1940. During this period substantial advances were made in basic knowledge related to oyster culture and to fish culture (including the effects of fertilizing water and of poisoning coarse fish), and to the relationship between fisheries and hydrography.

Dr. A. W. H. Needler was Director from 1941 until 1954, during the trying war years and the period of rapid expansion which followed. He was adept at perceiving specific economic needs of the Maritimes and the way in which the results of fisheries research could be applied to them. This led to increasing recognition of the Station's usefulness.

Dr. J. L. Hart became Director in 1954. His able and experienced staff are well qualified as consultants on most Maritime fisheries problems and contribute substantially toward developing fisheries policy.

Scientists

During the 50 years of its existence, more than three hundred students and scientists from the staffs of various universities and government departments have based biological research on the St. Andrews Station. Each has contributed his part in the growth of knowledge. The list below includes most of those who recorded profitable advances, whether as volunteer investigators or as employees of the Board. The list includes all the scientists who are currently employed by the Fisheries Research Board at the Station; these are marked thus (*). Among to-day's employees, the following six were associated with the Station 20 years ago: H. B. Hachey, Chief Oceanographer for Canada; C. J. Kerswill, in charge of salmon studies; A. H. Leim, in charge of taxonomic studies; R. A. McKenzie, herring investigator; J. C. Medcof, in charge molluscan shellfish investigation; M. W. Smith, in charge of trout investigations. One other scientist must be given special mention: H. C. White, whose unique abilities as an observer contributed to the Station's freshwater studies from 1927 until his retirement in 1955.

J. R. Adams
D. F. Alderdice
Armine Alley
H. M. Allan
Marion Anderson
C. W. Andrews

B. P. Babkin
L. W. Bailey
*W. B. Bailey
W. H. T. Baillie
A. D. Bajkov
Helen I. Battle
P. M. Bayne
S. A. Beatty
H. H. Bell
H. P. Bell
B. A. Bensley
Clara C. Benson
Ruby Bere
N. J. Berrill
P. Bjerkan
E. C. Black
W. F. Black
A. A. Blair
D. J. Bowie
E. L. Bousfield
T. Braarud
*Vivien M. Brawn
S. W. Britton
A. H. R. Butler
Frances M. Burwash

J. Campbell
*N. J. Campbell
A. F. Chaisson
*J. R. Chevrier
L. P. Chiasson
Lucy S. Clemens
W. A. Clemens
*A. E. H. Collin
J. B. Collip
A. R. Cooper
C. J. Connolly
G. G. Copeland
H. S. Coulthard
P. Cox
C. Helen Craw
E. H. Craigie
Mary E. Currie

E. Dahlgren
J. A. Dauphinee
Viola M. Davidson
*L. R. Day
D. B. DeLury
J. D. Detweiler
*L. M. Dickie
D. C. B. Duff
Dorothy Duff
G. L. Duff

Marjorie Ellis
*P. F. Elson

D. Fairchild
C. J. Fish
H. D. Fisher
*F. D. Forgeron
C. M. Fraser
M. H. Friedman
Clara W. Fritz
Nancy Frost

A. H. Gee
N. E. Gibbons
M. E. C. Giglioli
L. Gilchrist
H. Godfrey
J. N. Gowanlock
M. Graham
H. H. Gran
L. Gross

*H. B. Hachey
F. C. Harrison
*J. L. Hart
F. R. Hayes
Jean T. Henderson
E. Hess

J. Hjort
R. E. S. Homans
W. S. Hoar
A. Hunter
A. G. Huntsman
M. Elinor Huntsman

F. P. Ide

J. Jansen
F. S. Jackson
*Y. M. L. O. Jean
Anne M. Jeffers
G. W. Jeffers
F. Johansen
W. H. Johnson
W. G. Jones

*M. H. A. Keenleyside
*C. J. Kerswill
E. J. King
Hazel M. King
A. B. Klugh
A. P. Knight
*A. C. Kohler
S. A. Komarov

*L. M. Lauzier
*A. H. Leim
*J. E. H. Legaré
F. E. Lloyd
J. F. Logan
*R. R. Logie
T. M. Lothian
J. M. Luck

A. B. Macallum
E. W. MacBride
W. T. MacClement
*F. D. McCracken
N. A. McCormick
D. L. McDonald
R. H. M'Gonigle
D. G. MacGregor
F. C. McIntosh
Margaret E. MacKay
*R. A. McKenzie
*D. W. McLeese

H. J. McLellan
D. J. MacLeod
J. J. R. Macleod
J. P. McMurrich
N. A. McNairn

M. O. Malte
J. R. Martin
*W. R. Martin
W. H. Martin
J. W. Mavor
*J. C. Medcof
F. R. Miller
D. H. Mills
P. L. Montreuil
Bessie K. E. Mossop
Irene Mounce

Alfreda Berkeley Needler
A. W. H. Needler
J. Nelson
C. L. Newcombe
Dorothy Newton
J. V. V. Nicholls
E. C. Noble

Emma C. Odell

*J. E. Paloheimo
Jean R. Panton
Olive G. Patterson
D. P. Penhallow
C. E. Petite
H. G. Perry
H. Margaret Perry
Kathleen F. Pinhey
*P. M. Powles
E. E. Prince

G. B. Reed
Margaret E. Reid
Christine E. Rice
F. A. H. Rice
A. D. Ritchie
H. M. Rogers
A. D. Robertson

W. Sadler
*J. W. Saunders

W. R. Sawyer
D. M. Scott
Eleanor Shanley
Barbara L. Shaw
Evelyn B. Shaw
H. P. Sherwood
R. G. Sinclair
W. W. Simpson
G. F. Sleggs
G. F. M. Smith
*M. W. Smith
Verna Z. Smith
G. M. Somerville
M. I. Sparks
C. Marion Spence
*J. B. Sprague
J. Stafford
D. H. Steele
J. A. Stevenson
V. Stock
Charlotte M. Sullivan

A. R. A. Taylor
W. Templeman
L. W. Thurber
*S. N. Tibbo
*R. W. Trites

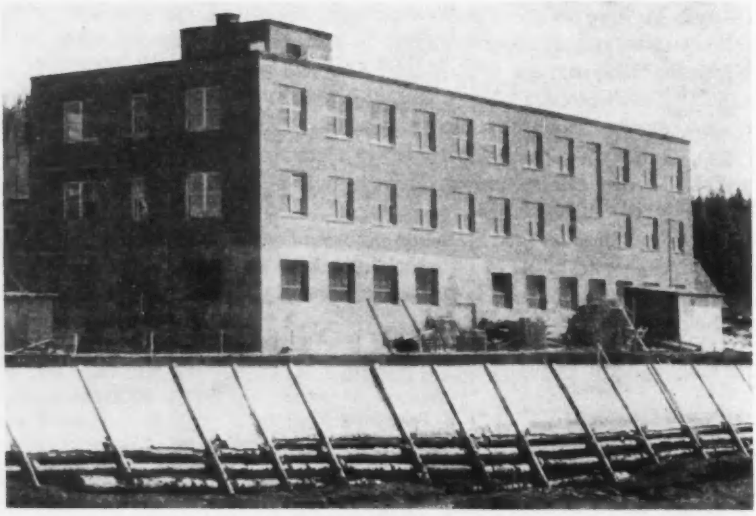
A. Vachon
V. D. Vladykov

E. M. Walker
S. J. Walker
N. A. Wallace
F. E. Warburton
Althea E. Warren
H. Wasteneys
E. E. Watson
H. C. White
*D. G. Wilder
A. Willey
C. B. Wilson
Helen I. Wilton
Margaret H. Wilton
R. P. Wodehouse
R. W. Wolfgang
R. Ramsey Wright

Non-Scientific Employees

The scientists and student assistants attached to the Station have been ably supported by a great many employees representing a wide variety of skills. Each has filled his role but a few merit special mention. First in both time and

contribution are Captain A. E. Calder who, as engineer, captain and collector, remained in the employ of the Station from 1909 until 1950, and Captain E. G. Rigby who from 1916 until 1919 was captain of the *Prince* and from 1921 until his retirement in 1951 was in general charge of vessels and the shore plant as collector and curator. Like his successor, H. Y. Brownrigg, who started with the Station in 1930 and is still with it, he helped unmeasurably in meeting the scientists' needs for collections and equipment. In the early days of the Station



Extension to the main laboratory building nearing completion, 1958.

the secretarial duties were discharged by Miss M. S. Rigby and her conscientious efficiency made it possible for the Director to devote most of his time to scientific work. Others whose efforts contributed substantially to the work of the Station through the years are: J.'G. Clark, K. W. Johnston, G. Herbert Lamb, D. A. Stinson, Frances L. Stinson, and C. S. Tucker.

VESSELS

As the St. Andrews Station has from the first been essentially a marine station, boats have always been an important part of the equipment. In 1908 two vessels were in use, the 35-foot *Sea Gull* and the 24-foot *Sagitta*. The former was used for six or seven years, the latter was not disposed of until 1940. The next acquisition was the *Edward E. Prince*, generally referred to as the *Prince*. She was 50 feet long as built in 1913 but was rebuilt and lengthened to 60 feet in 1916. She was lent to the International Passamaquoddy Fisheries Commission and retired at the conclusion of field work in 1932. Other vessels

have been used for longer or shorter periods, viz., *Delphine*, 28.6 feet long, acquired 1916 and disposed of in 1942; *Zoarces*, 90 feet long, acquired 1931, transferred to the Navy in 1940; *Ahic*, 42 feet long, acquired 1945, disposed of in 1948; *Gulf Explorer*, 45 feet long, acquired 1946, disposed of in 1956; *Mactra S.*, 40 feet long, acquired 1946, disposed of in 1950; *Pandalus*, 40 feet long, acquired 1946, disposed of in 1953. The remaining boats are still in service. They are: the 32.2-foot *Clupea H.*, built in 1942, the 70-foot *J. J. Cowie*, built in 1943, the 84.5-foot *Harengus*, built in 1946, the 53.8-foot *Mallotus*, built in 1951, the 50-foot *Pandalus II*, acquired in 1954, and the 34.8-foot *Cyprina*, built in 1955. For the most part these are versatile vessels, effectively carrying out a wide range of fisheries and hydrographic operations. The *Clupea H.* is now attached to the Ellerslie sub-station. The *Cyprina* is a specially built broad shallow-draft vessel to accommodate an experimental mechanized clam digger in work over clam flats.

ACCOMMODATION

The progress of a research station's work depends primarily upon its objectives and upon the people doing the work but cannot be entirely divorced from the conditions under which the work is carried out. At the St. Andrews station the research has nearly always been ahead of the accommodation. This has produced some discomfort and occasional hardship but has illustrated the continuing effort to apply resources direct to research.

At St. Andrews, the laboratory building and the residence building were both put up in 1908. The laboratory was a wooden structure looking much like the current old wing of the main laboratory structure. In 1922 the laboratory was enlarged with an addition on the seaward end. In the following year the residence was expanded. Summer living accommodation had been also increased in 1916 by the construction of a double cottage and was extended again in 1927 by the construction of a second double cottage. On March 9, 1932, the laboratory building was completely destroyed by fire with the insupportable loss of the library and valuable records. Reconstruction was started immediately and by 1933 a new fire-proof building much resembling the old original structure in plan was in use. In the 1940's the two pairs of cottages were prepared for winter occupancy and they served a useful purpose in providing permanent staff members with living quarters until they could find suitable accommodation in the town. In 1930 a hatchery building was constructed with a basement fitted for experimental work in fish culture. The upper storey at first provided space for the staff of the International Passamaquoddy Fisheries Commission and was later redesigned for general use. In 1951 one part of a double cottage was turned into office space to provide temporary accommodation for the headquarters of the International Commission for the Northwest Atlantic Fisheries. In 1954 the whole building was redesigned in order to meet the growing need for laboratory accommodation. It was occupied by the oceanographers. In 1956 the remaining two cottages were altered to provide laboratory and office space for the growing groundfish and herring investigations.

The responsibility of the Station to deal with fish problems throughout the Maritimes has necessitated establishing more or less permanent substations from time to time. These have been provided by the Department of Public Works, by rough construction, or by special arrangement. The oyster research station at Ellerslie, built in 1930 and still in operation, calls for special mention.

A large extension on the main laboratory at St. Andrews is under construction in 1958. It will provide good laboratory facilities and fire-proof accommodation for the present scientific biological staff.

CONCLUSION

This account attempts to give in condensed form the important trends and developments in fisheries research at the St. Andrews Station. In condensation, inaccuracies may have been introduced and important events and names may have been omitted. For some years available records are incomplete and this fact too may have led to important omissions.

I have been helped in its preparation by my senior colleagues named above, and to them I am very grateful as I am to Mr. L. R. Day who has given invaluable assistance in completing this account. I have leaned heavily upon an unpublished compilation on the "Biological Stations of Canada" by Miss M. S. Rigby and have plagiarized freely. Without that account it would have been impossible to attempt the present history.

IMPORTANT DATES IN THE HISTORY OF THE ST. ANDREWS BIOLOGICAL STATION

1899	Board of Management (later Board of Directors) set up.
1899–1900	Portable laboratory at St. Andrews.
1902	First volume of *Contributions to Canadian Biology* published.
1908	Shore-based research started with Dr. D. P. Penhallow, Director.
1912	Biological Board Act passed.
1912	Dr. A. G. Huntsman appointed Curator; 1921, Director. (Acting Curator in 1911, and investigator in 1910.)
1913	M.V. *Edward E. Prince* available.
1914–1915	Canadian Fisheries Expedition.
1917	Cheticamp Expedition to the southeastern Gulf of St. Lawrence.
1918	Miramichi Expedition.
1918	First *Bulletin of the Biological Board of Canada* published.
1921	North American Council on Fishery Investigations established.
1923	Belle Isle Strait Expedition.
1924	Technological investigations transferred to Halifax, N.S.
1930	Hudson Bay Fisheries Expedition.
1930	Sub-station established for oyster investigations, Ellerslie, P.E.I.
1931	International Passamaquoddy Commission.
1931	*Progress Reports* of the Atlantic Coast Stations commenced to be published.

1931 M. V. *Zoarces* available.
1932 Main building destroyed by fire.
1933 North American Council on Fishery Investigations met at St. Andrews.
1934 Dr. A.H. Leim, Director.
1937 Fisheries Research Board Act passed.
1941 Smelt laboratory established at Chatham, N.B.
1941 Dr. A.W.H. Needler, Director.
1942 General Series of *Circulars* started.
1943 M.V. *J. J. Cowie* available.
1944 Atlantic Herring Investigation Committee established.
1946 M. V. *Harengus* available through the Department of Fisheries for AHIC work. 1957, transferred to the Station.
1946 Joint Committee on Oceanography established, Atlantic Oceanographic Group set up.
1946 Field station, brook trout investigations, Ellerslie, P.E.I., established.
1948–1950 Dr. A. W. H. Needler on partial leave as Assistant Deputy Minister of Fisheries; Dr. D.G. Wilder Assistant Director for the same period.
1949 Federal–Provincial Co-ordinating Committee on Atlantic Salmon established.
1950 Miramichi salmon unit established.
1951 Groundfish statistical unit established at Halifax, N.S.
1952 Statistical Series of *Circulars* started.
1951 International Commission for the Northwest Atlantic Fisheries (ICNAF) established, with temporary headquarters at St. Andrews.
1952 Meeting of ICNAF at St. Andrews.
1954 Station supplied oceanographic staff to H.M.C.S. *Labrador* in its circumnavigation of North America.
1954 Dr. J. L. Hart, Director.
1956 International Passamaquoddy Fisheries Board established.
1958 Federal–Provincial Atlantic Fisheries Committee established, superseding the Co-ordinating Committee on Atlantic Salmon.

On the Dominant Flow in the Strait of Belle Isle[1]

By W. B. Bailey
Fisheries Research Board of Canada
Atlantic Oceanographic Group, St. Andrews, N.B.

ABSTRACT

In addition to the usual tidal currents in the Strait of Belle Isle, there is, at times, a tendency for the current to set in one direction more than in the other. This over-balance of water movement in one direction is termed the element of dominant flow. The possible causes of this flow are attributed to meteorological factors and to others effecting long-period fluctuations in sea level.

Very few extended oceanographic observations have been available to illustrate this phenomenon on a grand scale, particularly for a westerly flow. Observations taken in September 1955 illustrate a dominant westerly flow in considerable detail. This dominant flow was associated with the passage of an intense low pressure area (Hurricane Ione) from the Gulf of St. Lawrence to the Labrador Sea between September 21–23, 1955.

INTRODUCTION

Although the Strait of Belle Isle lies on the Great Circle track between the Gulf of St. Lawrence and central United Kingdom ports, very few extended oceanographic observations have been available to illustrate the phenomenon of dominant flow on a grand scale. The addition of recent oceanographic data to those already accumulated permits a fuller description of the oceanography of the region and a better insight into the possible causes of the dominant flows.

The Strait of Belle Isle

The Strait of Belle Isle (Fig. 1), lying in a NE–SW direction between the northern coast of Newfoundland and southern Labrador, joins the northern portion of the Gulf of St. Lawrence to the Atlantic Ocean. The strait has a length of about 73 miles (118 km.) measured from the south end of Belle Isle to abreast of Greenly Island near the Labrador coast. It has a width of 10 to 18 miles (16 to 29 km.) for 50 miles (80 km.) of its length, beyond which it widens rapidly in both directions. At its narrowest part the depth of water does not exceed 35 fathoms (84 m.), while a maximum depth of 80 fathoms (146 m.) is found midway between Belle Isle and the Labrador coast. However, the average depth is approximately 40 fathoms (73 m.). The north shore of the strait is bold and the water off it is deep, whereas the south shore is low and sloping, but depths drop rapidly to 30 fathoms (54 m.).

The Element of Dominant Flow

While carrying out current measurements in the Strait of Belle Isle during the summers of 1894 and 1906, Dawson (1907) noted that in addition to the

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regular flood and ebb of the tides through it, there was almost always a tendency for the current to set in one direction more than in the other. This over-balance of water movement in one direction was termed the element of dominant flow, which is superimposed upon the usual tidal fluctuations.

The character of the flow is such that it frequently flows in one direction for several days before reversing, but at times it may continue to flow in one direction for a week or more (Dawson, 1907). The maximum observed velocity for a dominant flow westward was 1.7 knots (88 cm./sec.), while for an eastward flow it was 1.4 knots (72 cm./sec.). During periods of weak tidal currents the strength of the dominant flow has been observed to be sufficiently great to reverse the direction of the usual tidal stream with a net current of 1.4 knots (72 cm./sec.) (Dawson, 1907).

The General Circulation

At the eastern approaches to the Strait of Belle Isle, the water movements are dominated by the southeastward-flowing Labrador Current. At times, part of the inshore branch of this current enters the strait along the Labrador Coast, and at times it is joined by a movement out of the Gulf of St. Lawrence along the coast of Newfoundland (Smith *et al.*, 1937). At the western approaches to the strait, a fairly definite current has been described flowing northeastward along the west coast of Newfoundland. Part of this northeastward flow is deflected by the Mecatina Bank and crosses to the Quebec coast where it is joined by a southwestward flow that may have had its origin in the Strait of Belle Isle. Investigations have shown the circulation of the waters in the strait to consist of (a) a progressive inward movement of Labrador coastal water on the north side, (b) a progressive outward movement of Gulf of St. Lawrence water on the south side, (c) a dominant outward flow of gulf water (Huntsman *et al.*, 1954) and (d) a dominant inward flow of Labrador coastal water (Bailey, MS, 1957).

OCEANOGRAPHIC CONDITIONS DURING DOMINANT FLOWS

Dominant Flow Easterly

The results of the oceanographic observations taken by the 1923 Strait of Belle Isle Expedition on September 7, 1923, in the narrower portion of the strait afford a more complete picture of the horizontal distributions of temperature and salinity than has previously been the case. The observations indicated a prominent and dominant northwesterly flow outward from the Gulf of St. Lawrence. The picture is considerably enhanced by the horizontal distributions of temperature and salinity of Fig. 2 (after Huntsman *et al.*, 1954). Water of temperatures higher than 0.0°C. occupied the strait, with warmer water (as high as 11.0°C.) being quite prominent to depths of 50 m. The flow of Labrador coastal water of comparatively lower temperatures seems, from the trend of both isotherms and isohalines, to be diverted through the passage between Belle Isle and Newfoundland.

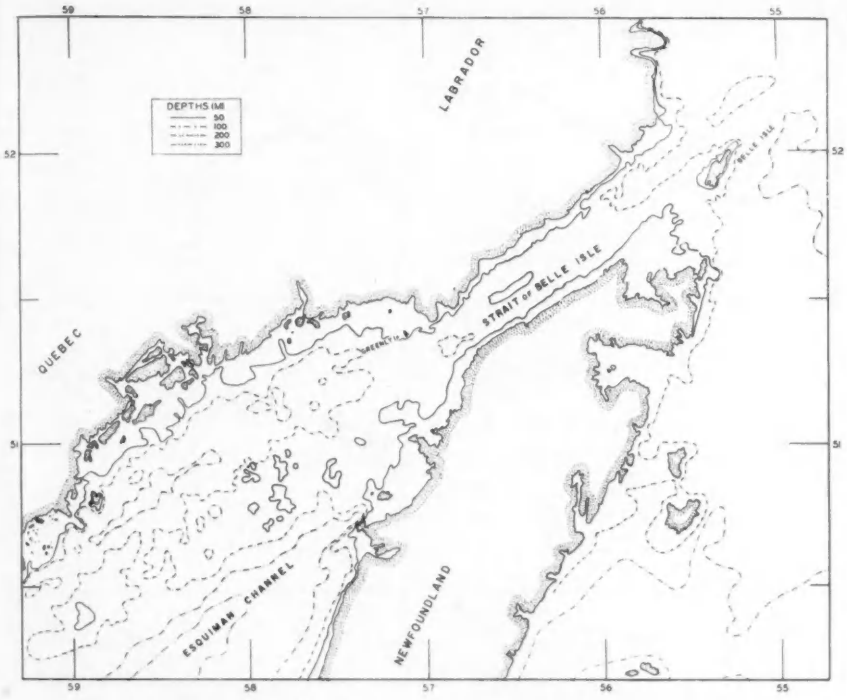

FIG. 1. The Strait of Belle Isle and its approaches showing the bottom configuration.

DOMINANT FLOW WESTERLY

In September 1955 a network of oceanographic stations was occupied in the Strait of Belle Isle and its approaches, as part of a large-scale survey of the waters around Newfoundland. The results of this survey in the strait presented in considerable detail for the first time the oceanographic conditions attendant to a dominant flow westward of Labrador coastal water into the Gulf of St. Lawrence. The details of the horizontal distributions of the temperature and salinity during the period September 23–25, 1955, are given in Fig. 3 and 4. In these diagrams, the presence of water with temperatures between 3 and 5°C. and with salinities less than 32.0‰, extending from the Labrador coast through the strait, indicates a dominant westward flow which appears to assert a considerable influence on the distribution of temperature and salinity in the northeastern part of the Gulf of St. Lawrence.

METEOROLOGICAL CONDITIONS DURING DOMINANT FLOWS

Dawson (1907, p. 29), in discussing the greatest dominant flows observed in two seasons in relation to weather conditions, gave several examples, two of which are as follow on p. 1167.

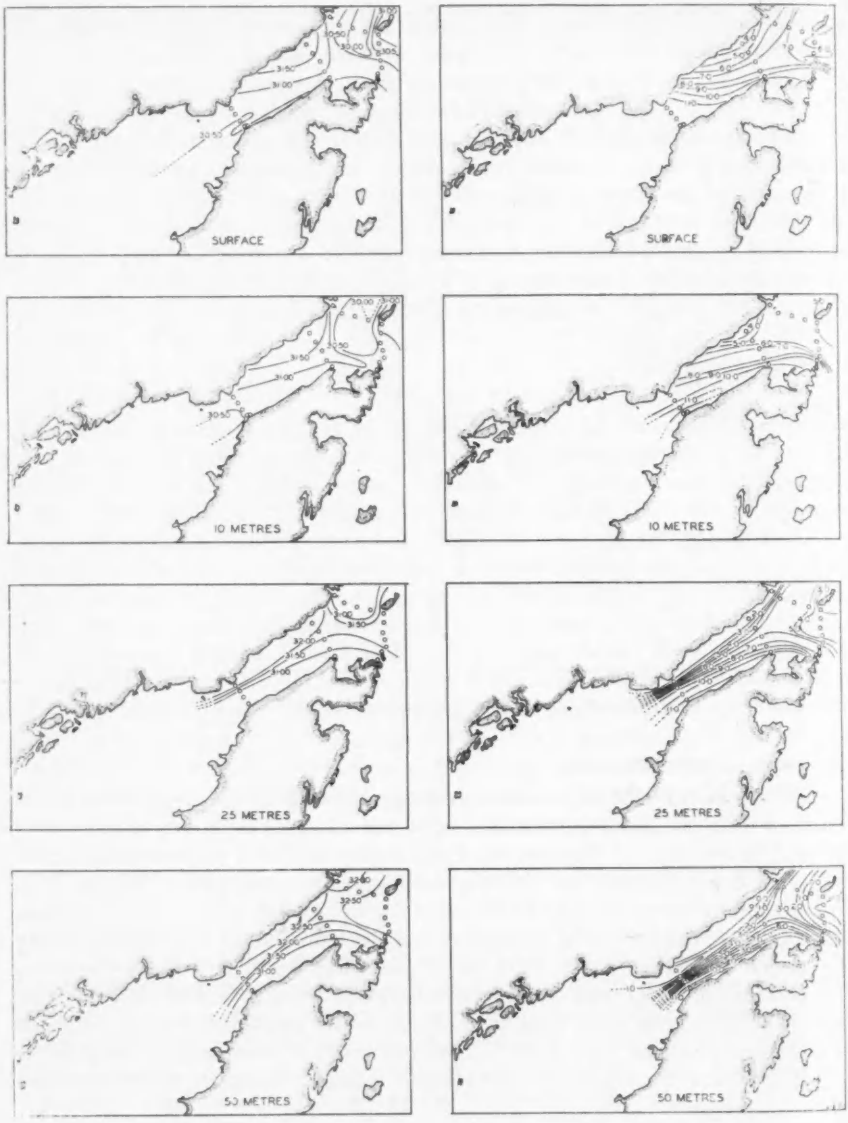

FIG. 2. Distributions of temperature and salinity in the Strait of Belle Isle, September 7, 1923, (after Huntsman, Bailey and Hachey, 1954).

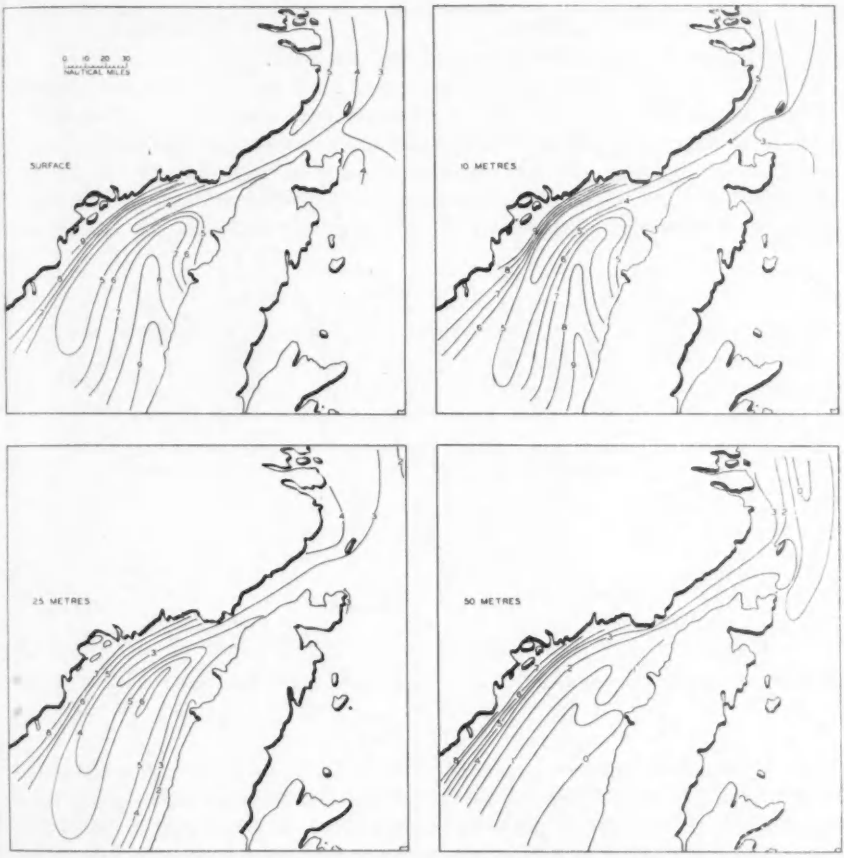

FIG. 3. Distribution of temperature in the Strait of Belle Isle region, September 23–25, 1955.

DOMINANT FLOW EASTWARD

"In the season of 1906, the most marked period of dominant flow to the eastward occurred at the end of July . . . From July 30 to August 2, during 70 hours, the current ran almost continually eastward, either turning only once in the 24 hours or not turning at all, but only slackening during the flood period. The greatest velocity eastward was 2.76 knots, during ebb tide.

"These days began with fog and rain and the barometer at 29.70. The weather gradually cleared, and the barometer rose slowly and steadily to 30.15 by noon on August 3, when easterly weather set in. The wind during these days was variable at first, but settled into the west and north-west, rising on the 3rd to 35 miles an hour."

DOMINANT FLOW WESTWARD

"The best example in 1894 of a dominant westward flow through the strait, occurred from September 5 to 8. All the indications concurred in showing that the

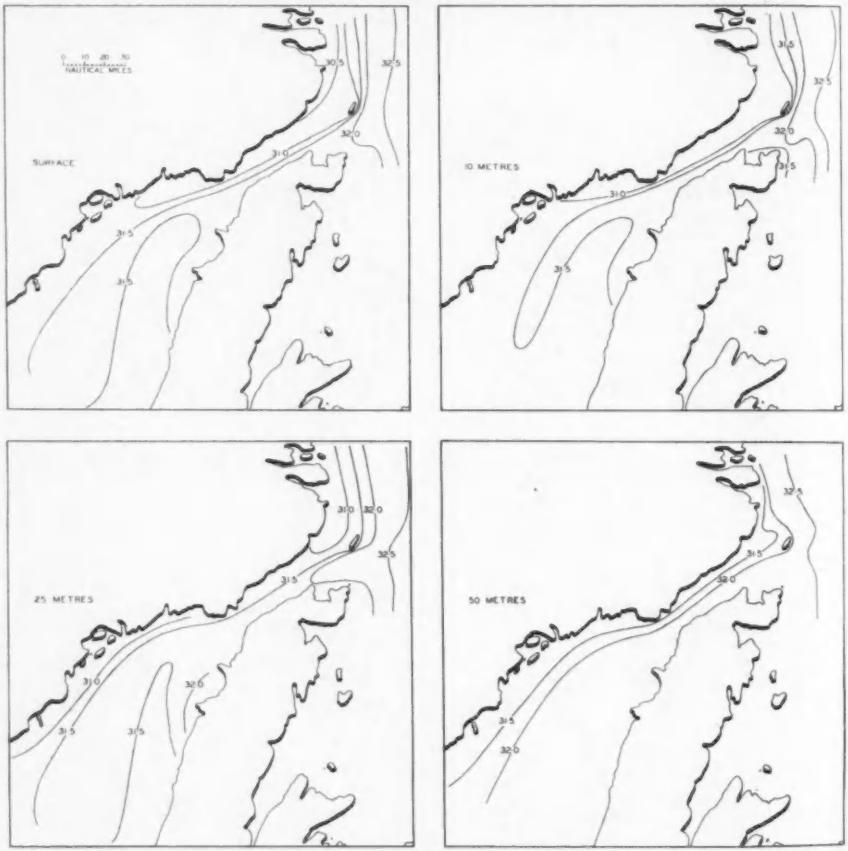

FIG. 4. Distribution of salinity in the Strait of Belle Isle region, September 23–25, 1955.

current ran continuously in the one direction during these days; although the observations were much interrupted by bad weather. There were also about a dozen icebergs seen in the strait during this time; and their motion agreed with the regular observations in showing that the current ran continuously westward. The current then varied from a minimum of 0.54 knots to a maximum of 3.15 knots, in the one direction . . .

"During this continuous westward flow, the conditions of wind and barometer were disturbed and complicated, as a storm centre was passing over the northern part of Newfoundland at the time. The low pressure area of this storm centre was over the Gulf during the 5th and was nearest to the strait on the morning of the 6th, on its way eastward to the Atlantic. From the morning of the 5th till the evening of the 8th, there were 60 hours of N.N.W. wind averaging 25 miles an hour, and rising at times to 45 miles. During the remainder of the time the winds were light and variable. The westward flow thus took place at a time of severe disturbance due to the proximity of a storm centre."

HURRICANE IONE, 1955

In September 1955, Hurricane Ione passed in a northeast direction over the central portion of Newfoundland, being centred over the island on the 21st. Winds associated with this storm were reported to be greater than 100 m.p.h. The influence of this severe tropical storm was felt in the Belle Isle region for 2 days, and on the day following its passage, winds in the area were still quite strong. Copies of the weather maps of the United States Weather Bureau for September 21, 22 and 23, 1955, are shown in Fig. 5. Immediately following the passage

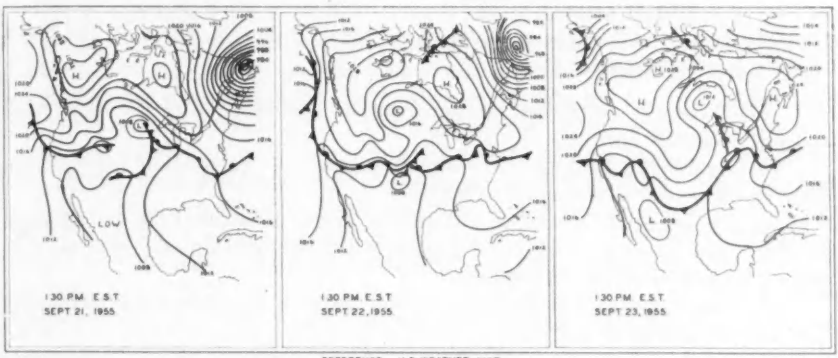

FIG. 5. Weather maps for North America illustrating the atmospheric pressures at sea level.

of the storm the survey by C.N.A.V. *Sackville* was carried out, the results of which were discussed in connection with the horizontal distribution of properties as illustrated in Fig. 3 and 4. A comparison of these diagrams with the pressure fields shown in Fig. 5 suggests a close association between the wind system and the dominant flow in the Strait of Belle Isle.

CAUSES OF DOMINANT FLOWS

Observations and studies made by Dawson (1907) indicated that dominant flows were related to fluctuations in mean sea level, which took place over long periods. Montgomery (1938) investigated the causes of long-period fluctuations in mean sea level at two stations on the United States Atlantic coast and concluded that of the eight factors which may create long-period fluctuations in mean sea level, only four were of importance, namely:

(a) Dynamic effects due to variations in gradient currents:
  (i) caused by variations in nearby major ocean currents,
  (ii) caused by action of the wind in creating a gradient current (stream-effect).

(b) *Windstau* (wind-effect). The action of the wind in moving waters along its direction.

(c) Widespread effects due to the action of one or more factors acting at a distance.

(d) Steric oscillations due to seasonal changes in the specific volume of the waters.

In Montgomery's (1938) study the effects of changes in the atmospheric pressure were compensated for in the observational data and thus were not considered as contributing factors.

Some results of Dawson's careful investigation of many of these factors in attempting to determine the cause of the element of dominant flow in the Strait of Belle Isle region are as follows:

(a) There was no evident relation between the direction of the local wind and the dominant flow.

(b) Analysis of tidal data showed that there was no relation between the dominant flow and astronomical causes.

(c) The mean sea level in the strait was raised or lowered for several days at a time. The harmonic analysis of 3 years of tidal records revealed that no tide of long period could be distinguished.

(d) There appeared to be some relation between the direction of dominant flow and the season of the year.

(e) Investigations of meteorological causes indicated that a barometric gradient which lay northward (high-pressure region to the south) across the Gulf of St. Lawrence and along the east coast of Newfoundland corresponded to an eastward dominant flow through the strait. Conversely, a gradient which lay southward (high-pressure area to the north) corresponded with a dominant flow westward.

Dynamic Effects

The dynamic effects due to fluctuations in the gradient currents are difficult to assess without an extensive series of observations. In the Strait of Belle Isle changes in the strength of the Labrador Current, which flows past the eastern end of the strait, may well contribute to the element of dominant flow. Similarly, changes in the rates of circulation of the Gulf of St. Lawrence, and the Esquiman Channel in particular, may further the development of a dominant flow. However, the causes of the fluctuations in these currents are not well understood and may be linked closely to some of the other factors under consideration, most notable of which is the influence of the wind in producing a gradient current (stream-effect). Montgomery (1938) concluded that the stream-effect of *Windstau* is to a large extent indistinguishable from the dynamic effect.

Wind-effects

The influence of the wind in raising or lowering the mean sea level in a short period of time has been demonstrated at many stations along the Atlantic

coast of North America. Amplitudes of 0.3 m. appear to be common and as much as 0.52 m. in strong gales (Hachey, 1934; Montgomery, 1938; Trites, MS, 1951; Longard and Banks, 1952; Miller, 1957).

Theoretical and empirical considerations of the influence of the winds on water movements agree that the transport of water will be about 45° to the right of the wind direction in the Northern Hemisphere (Sverdrup *et al.*, 1942). Miller's (1957) observations at Atlantic City, N.J., indicated that the maximum effect of the winds in raising or lowering sea level was produced when the winds were inclined at an angle of 50° to the coastline.

In the Strait of Belle Isle region and along the Labrador coast, winds from NNE to NW will tend to favour the southeastward flow of water in the Labrador Current and to increase the sea level along the Labrador coast. Winds from these same directions will tend to lower the sea level in the Esquiman Channel. Alternately, winds from the SW quadrant will tend to raise the sea level in the Esquiman Channel and lower it on the Labrador side of the strait. The amount of elevation or depression by a given wind system will be modified considerably by the topographical features of the region, affecting both winds and sea currents.

It is evident that winds blowing over the region are capable of creating large differences in sea level between the regions at the end of the Strait of Belle Isle. Some amplification to this is given by the casual observations of residents in the central part of Belle Isle area, who state (according to Dawson, 1907) that the highest tides occur with winds from the northerly quarter, while the lowest tides occur with winds from the west and southwest.

Effects of Changes in Atmospheric Pressure

Changes in atmospheric pressure cause the sea surface to behave much like an inverted barometer. Higher air pressures depress the sea level, and lower air pressures elevate it. In general, an increase of 1 mb. in atmospheric pressure will cause a depression of 1 cm. in sea level. In the Strait of Belle Isle, the element of dominant flow could be caused by atmospheric pressure differences over the waters at the ends of the strait. However, some consideration of these effects indicates that they would be relatively small in comparison with those caused by winds.

Steric Oscillations

Changes in the height of the sea surface due to seasonal variations of specific volume are called steric oscillations (Patullo *et al.*, 1955). The temperature and salinity of the waters in the regions at the ends of the Strait of Belle Isle are quite different as shown in Fig. 2, 3 and 4, which suggests the possibility that steric oscillations could give rise to a tendency for dominant flows to take place. However, the fluctuations in this region, according to Patullo *et al.* (1955) are small in comparison with those due to the effects of winds. At the present time data are too few to indicate any more than a possibility of a dominant flow resulting from steric oscillations. In general, it would be expected that differences in steric oscillations between the ends of the strait would tend to modify existing dominant flows rather than cause them.

Widespread Effects

The action of the several factors which are considered capable of creating fluctuations in mean sea level at some distance from the Strait of Belle Isle undoubtedly makes some contribution to the element of dominant flow. By and large, it must be considered that the widespread effects will influence the seasonal trends in the direction of the dominant flows, rather than cause the more spectacular high-velocity currents that have been so readily observed.

DISCUSSION

The most promising results in relating the direction of dominant flow to meteorological factors were given by the direction of the barometric gradient in a north–south (330–150° True) direction across the Gulf of St. Lawrence and the east coast of Newfoundland (Dawson, 1907, p. 28):

> "This indication is confirmed by the weather conditions at the time that the greatest dominant flow occurred in each of the two seasons. . . . When the greatest eastward flow occurred, the barometer was high and steady, with a gradiant lying northward from a high pressure area to the south. The greatest westward flow occurred after gales from the north and northeast, caused by a low-pressure storm centre passing across Newfoundland, south of the strait; occasioning a pronounced gradiant southward . . ."

Further consideration of the two examples presented by Dawson with regard to the wind system as well as the pressure distribution leads to some interesting results. Figure 6 shows the general schematic pressure systems mentioned by him and quoted previously on page 1167. Since the winds tend to blow at an angle of about 20° to the isobars, southwesterly winds (W in the Figure) are

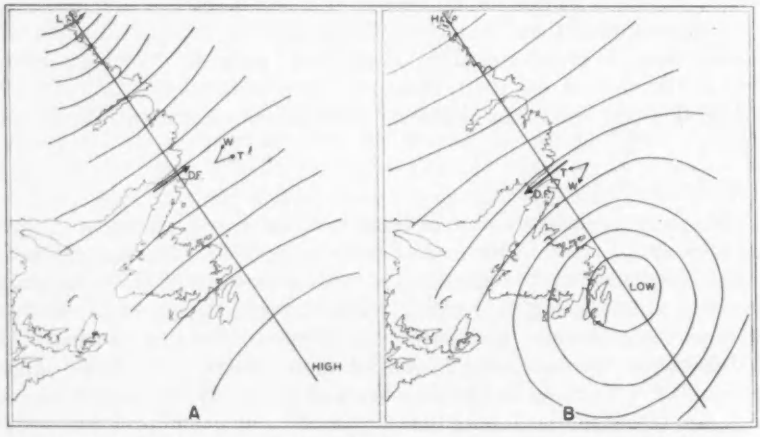

Fig. 6. Schematic diagrams of atmospheric pressures at sea level as described by Dawson (1907) during a dominant flow eastward (A) and during a dominant flow westward (B).

produced in the first case and northeasterly winds (W) in the second. The average deflection of the wind current (T) from the direction of the wind is about 45° to the right (Sverdrup *et al.*, 1942, p. 494). Applying these principles to the above examples, it appears in the case with the gradient northward (Fig. 6, A) that the winds drive the waters into the narrowing Esquiman Channel along the west coast of Newfoundland. The direction of the barometric gradient is indicated by the heavy diagonal lines. At the eastern end of the Strait of Belle Isle, the winds are off-shore, which tends to depress the sea surface, further expanding the difference in sea level between the ends of the strait. A wind system of this type tends to produce a dominant eastward flow, and such was observed by Dawson. The schematic pressure system as shown indicates that there is only a minor difference in atmospheric pressure between the areas at the ends of the strait. Thus under a set of conditions of this type, it appears that differences in atmospheric pressure will have little effect in creating a dominant flow.

In the second case, with a low-pressure area located off the southeast coast of Newfoundland (Fig. 6, B), the winds would blow from north to northeast, depending on the intensity of the low-pressure area. The wind currents would be southeastward along the Atlantic coasts of Labrador and Newfoundland and southwestward along the Quebec shore in the Esquiman Channel. A situation such as this favours a dominant westward flow, and such was observed by Dawson.

As in the first case, the isobars would run along the axis of the Strait of Belle Isle and thus atmospheric pressure differences over the waters at the ends of the strait are of little account in causing a dominant flow.

Dawson noted that the westward dominant flow occurred after the subsidence of the strong wind in the Strait of Belle Isle and intimated that the dominant flow could not have been a wind-driven current. This would be so if the current were pure wind-effect rather than a stream-effect, as noted by Palman (1932). Miller (1957) reported that at Atlantic City, N.J., there was a mean time lag of 12 hours between equilibrium of the sea level and the state of the wind. The decay of the dynamic gradients built up by the winds depends upon the wind system which follows the main disturbance. Thus a dominant flow once established may be maintained in a given direction by a relatively weak wind field with the velocity of dominant flow somewhat reduced from that initially started.

With the very limited amount of data available, the relations between the winds and dominant flows appear to give a reasonable explanation as to the primary cause of the dominant flow. Certain modifications to the dominant flow may be brought about by changes in the atmospheric pressure, by differences in steric fluctuations between the ends of the Strait of Belle Isle, and by widespread effects of various factors acting in large areas of the Atlantic Ocean. At the present time, data are too limited to give much more than a rough indication that these factors may play a secondary role in creating adjustments to the dominant flows in the strait.

SUMMARY

1. The possible causes of dominant flows in the Strait of Belle Isle may be attributed to the following factors:
   (a) Dynamic effects due to fluctuations in the gradient currents at the ends of the strait.
   (b) Effects of wind.
   (c) Fluctuation in atmospheric pressure.
   (d) Steric oscillations due to changes in the temperature and salinity of the water.
   (e) Widespread effects due to the actions of the above at a distance over large areas.
2. Analysis of several examples of dominant flows indicates that the cause is due primarily to the effects of winds blowing in the strait region and not in the strait alone.
3. Atmospheric pressure changes are indicated as having only a secondary effect in creating a dominant flow.
4. Steric oscillations and widespread effects are indicated as having some seasonal influence on the dominant flow.

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The Discoloration of Foxe Basin Ice[1]

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ABSTRACT

The discoloured appearance of Foxe Basin ice has been a continuous subject of controversy since Baffin described the condition of this ice in 1615. A number of explanations are reviewed and discussed in view of the recent findings of H.M.C.S. *Labrador* in Foxe Basin.

A study of the problem was undertaken in relation to the oceanographic features of Foxe Basin. The results of these surveys have led to a theory of suspension-freezing of bottom sediments during the winter. Analyses of ice and bottom sediments support the theory that the dirt embedded in the ice is a marine sediment as opposed to wind-blown terrestrial particles.

INTRODUCTION

Foxe Basin is located within the southern limits of the Canadian Arctic Archipelago almost bordering on Hudson Bay (Fig. 1). The basin is bounded to the north and east by Baffin Island and to the west by Melville Peninsula and Southampton Island (Fig. 2). Access to the ocean is through Foxe Channel and Hudson Strait in the south. At the northern end, Fury and Hecla Strait provides a passage from Foxe Basin to the Gulf of Boothia, Prince Regent Inlet, and Lancaster Sound. The basin is a shallow inland sea of 65,000 sq. miles completely surrounded by Precambrian and Palaeozoic rock formations of granite and sedimentary deposits. The main part of the basin is a submerged continuation of the Palaeozoic regions around the eastern and western perimeters.

The sea ice of Foxe Basin is unique in the Canadian Arctic because it is distinguishable from nearly all other types of ice by its remarkable colour (Fig. 3). The ice is characterized by a uniform brown or buff-coloured layer of sediment which perennially appears on the surface of the winter floes.

The recorded history of this remarkable ice dates from the voyage of William Baffin in 1615 (Markham, 1881). Later in 1631, Luke Foxe encountered the same type of brownish-coloured ice in his explorations of Foxe Basin. The term "foxy ice" which is commonly used today to describe the dirty ice, is believed to have originated in Foxe's diary, but a typographical error in the marginal notes of his published account obscures positive identification of this interesting historical fact (Foxe, 1635). Since these two early expeditions, almost every ship which has visited Foxe Basin or Foxe Channel has reported a similar dirty state of the ice (Drage, 1748; Parry, 1824; Lyon, 1825; Wakeham, 1898).

Much speculation has arisen regarding the origin of the dirt and its composition, but few theories have accounted for all the facts. Baffin believed the ice to have formed near shore, but others have favoured the theory of deposition of dirt by winds (Low, 1906; Bell, 1885). The conclusion that the dirt is air-borne

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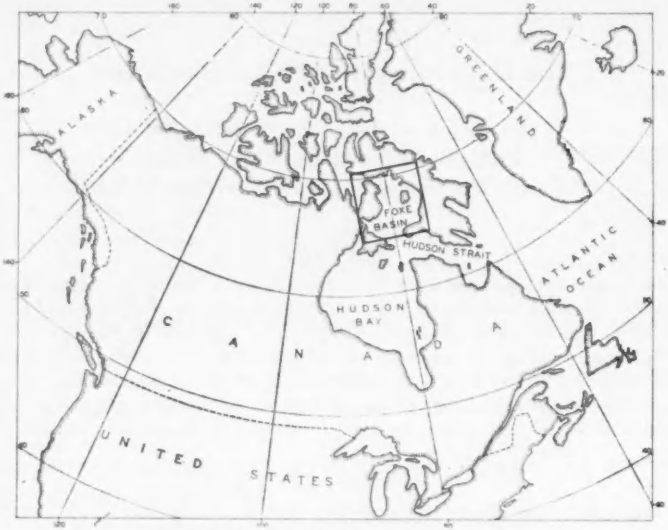


FIG. 1. Map of Canada, inset Foxe Basin

FIG. 2. Foxe Basin

FIG. 3. Foxe Basin ice showing discoloration and topography, Foxe Basin, 1955.

FIG. 4. A close-up view of dirty Foxe Basin ice, Foxe Basin, 1956.

FIG. 5. Clean ice floes off the east Baffin coast, 1955.

FIG. 6. Floe ice exhibiting gravel and rock falls, Peel Sound, 1957.

FIG. 7. An iceberg strewn with coarse gravel and stones, Hudson Strait, 1956.

FIG. 10. Dirty ice and sediment clouded water, Foxe Basin, 1956.

is not surprising because thousands of square miles of ice are affected (Fig. 3 and 4). What is surprising, however, is the speculation that has arisen over the attributable causes. Sir W. Parry (1824) was perhaps the most cautious in his explanation although he spent two winters in Foxe Basin. He states in his journal: "How these substances had been brought here in such abundance, another year's experience of the phenomena of these seas had not taught us to explain, and before we left this coast, we saw many hundred square miles of ice thus covered."

RECENT OBSERVATIONS

In 1955 and 1956, the Atlantic Oceanographic Group undertook an oceanographic survey of Foxe Basin on board H.M.C.S. *Labrador*. As part of this survey, the origin of the dirty ice was reconsidered in view of the many conflicting theories. These theories give consideration to air deposition of dirt and pollen, plankton growth, grounding of ice and fluvial deposition. From the results of the 1955 cruise, it became apparent that none of the above views fully accounted for all the characteristics of the ice, and the only explanations that showed promise stemmed from the oceanographic and geological conditions of the basin.

The circulation of Foxe Basin is dominated by a southerly flow along the western side and a counter-clockwise gyral in the central area south of Prince Charles Island. The southern flow of water along the western side of Foxe Basin and Foxe Channel transports water and ice into Hudson Bay and Strait (Campbell and Collin, MS, 1956). It is this movement of water that introduces the dirty ice into the Hudson Strait pack and finally the Labrador Coast pack ice.

In the winter, Foxe Basin is covered with severely hummocked ice, while in late summer, August and September, the ice generally disappears either by melting or transport to Hudson Bay or Hudson Strait.

The dirty ice presents several features which are unusual, the most obvious being its distribution throughout all of Foxe Basin and most of Foxe Channel during the ice season. In fact it is a rare occasion when one encounters clean ice. The few clean ice floes that are seen in the basin are so contrasting in their flat topography and white appearance, that they probably either invade the basin from Fury and Hecla Strait, or form in sheltered bays. In contrast, the dirty ice is nearly always hummocked, rafted, and well broken up into small and medium floes (Fig. 3 and 4). The general physical characteristics of the basin ice are much the same as old polar ice which has weathered after several seasons in the Polar Basin. The roughness and uneven topography of the ice has been claimed by some authorities to be the most severe in the Canadian Arctic. This characteristic is believed to be a phenomenon closely associated with the discoloration.

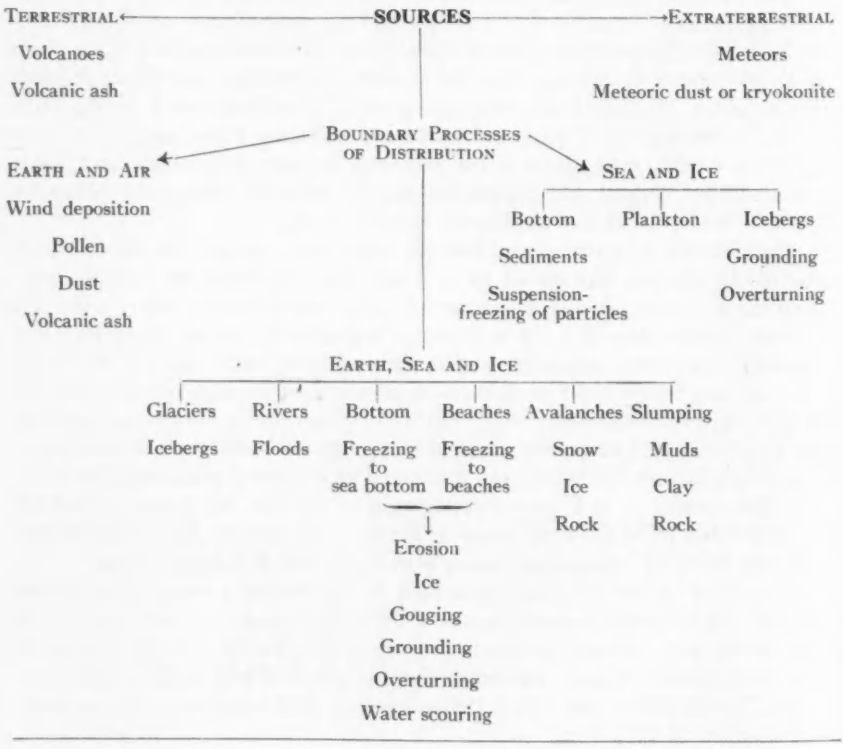
The colour of the ice varies depending on the surface concentration of the sediment, but its general appearance is a light olive brown or buff shade. The colour of the wet sediment occurs in the yellow hue of the Munsell system of colour classification. It has a numerical designation of 4Y4/2 for hue, value and chroma. The dry colour also falls in the yellow hue, with a corresponding numerical designation of 4Y7/1.

The sediments are fine-textured, varying on the average within a size limit of 0.005 to 0.5 mm. The dirt deposits are uniformly distributed over the ice surface giving rise to the "stained" or "soiled" appearance of the floes. Ice having this characteristic feature cannot be mistaken for ice that has grounded or overturned in shallow water and become strewn with debris such as seaweeds, rocks, and mud. For comparison, the sparklingly clean floes that one usually encounters off the Baffin Island coast are illustrated in Fig. 5. Two other illustrations (Fig. 6 and 7) are given of ice-borne sediments, gravel and rockfalls on ice, and an iceberg strewn with coarse gravel and stones.

MECHANISMS OF TRANSFER OF ICE-BORNE SEDIMENTS

The various sources, mechanisms and boundary conditions involved in most processes of ice-borne sediments are summarized in Table I. Many of these phenomena have been described in detail by Kindle (1924), but as far as Foxe Basin is concerned, he agreed with the views of Low.

TABLE I. Source and distribution of ice-borne sediments.



The only mechanisms that can satisfy the requirement of large-scale contamination of ice are plankton, meteoric dust, wind-borne particles, and suspension-freezing of sediments (Table I). Laboratory analyses, however, reduce the possibilities to only two mechanisms, wind-borne particles and suspension-freezing of sediments.

Microscopic and X-ray analyses revealed that the constituents of the dirt were basically inorganic and mineral. The floe sediments were quantitatively heterogeneous in mineralogy and size fractions, with particles of illite, quartz, biotite, and calcite being the most common. These minerals appeared fresh and unaltered chemically. On the basis of these results, the only two processes that can be considered as the likely sources of the dirt are wind and suspension-freezing of sediments.

Wind deposition has been considered as the most likely source of the dirt. The argument in favour of this hypothesis is based upon the fineness of the sediment and the large area of contamination (Low, 1906; Kindle, 1924; Kiernan, 1957).

Proponents of the wind theory consider two aspects of wind deposition, both of which are related to the seasonal periods of snow cover. To account for a winter formation of dirty ice in Foxe Basin, a large portion of the immediately surrounding terrain must remain bare, despite an average snowfall of 60 inches. Even with snow cover, it is still conceivable that wind scouring could take place and deposit sand, silt and clay over the ice. However, it is not so easy to envisage such a process occurring over some 50,000 sq. miles of Foxe Basin and not in other areas such as Committee Bay, where ice remains the year around, or the Gulf of Boothia or Hudson Bay.

The fact that winds are subject to change does not appear to have entered into the argument, although this phenomenon is known to give rise to banded layers of dirt in ice and snow (Crary, 1956). No evidence of banded layers of dirt has been observed with the Foxe Basin ice, and further, no accounts of discoloured snow either on the land or islands have been described by expeditions that have wintered in the basin.

The above arguments are perhaps answerable by assuming that the dirt is laid down in the spring when the snow cover has disappeared from the land. At first sight, this explanation appears realistic but examination of the ice and its geographical distribution cast doubt even on this view.

Cross-sectional and vertical corings of floe ice have revealed measurable quantities of dirt frozen in the interior. Small clear ice samples taken deep in the interior of freshly broken ice show that the dirt is randomly distributed within the ice, and generally in a flocculent form. Neither this evidence nor the occurrence of dirty Foxe Basin floes off Labrador in the spring support an argument of spring or summer deposition of dirt on the ice. The only conclusion that one can draw from these facts is that the dirt is trapped in the ice at the time of freezing.

The evidence of such a conclusion is the ice itself with its contaminated interior and soiled surface appearance. The fact that sediment is embedded in

the interior of the ice suggests the possibility that the mechanism is wholly a marine phenomenon.

It is suggested then that the bottom sediments are the source material of the ice-borne sediments, and that the forces of wind, waves, tides, and currents are sufficient to bring some of the sediments into suspension, at which point they can become frozen in the ice.

The conditions that this hypothesis must satisfy are the geophysical and historical facts that have been outlined; the most important of which are the distribution of dirt and absence of layers in the ice, the geographical limits of the formation of dirty ice, and the perennial appearance of dirty ice in Foxe Basin.

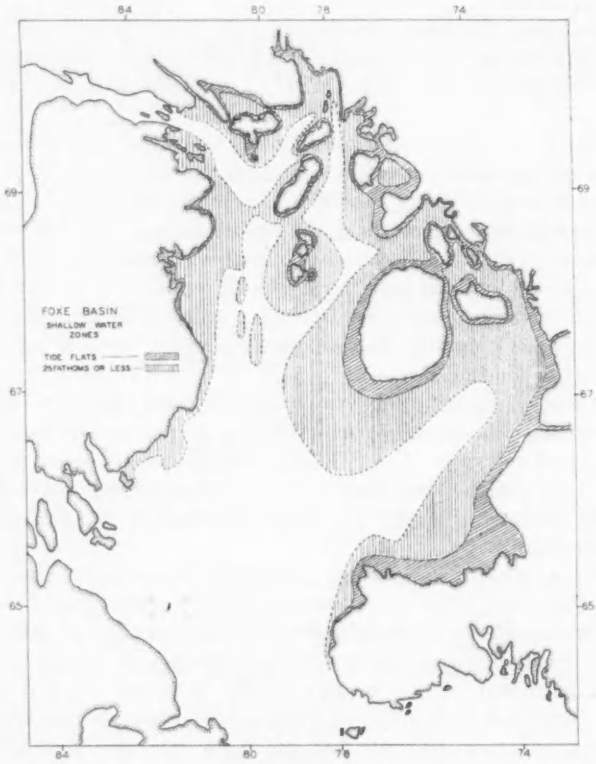


FIG. 8. Shallow water zones, Foxe Basin

SUSPENSION-FREEZING OF BOTTOM SEDIMENTS

Foxe Basin is extremely shallow throughout with extensive regions of exposed tidal flats (Fig. 8). The intertidal zone accounts for 6,000 sq. miles or approximately 10% of the basin area, while almost half of the total area lies within the

25-fathom contour. The shallowest areas are located in the southeastern section of the basin, including wide expanses of the sea bottom off Prince Charles Island and the Spicer Islands. In some of these localities, particularly Bowman Bay, the tide flats are very extensive, being 10 to 15 miles in width. On Bray and Prince Charles Islands and Baird Peninsula, the tide flats are 2 to 5 miles wide.

A tidal range of 20 to 30 feet is reported for Bowman Bay and 12 to 28 feet north of Baird Peninsula. The average tidal range in the northern half of Foxe Basin is 3 to 12 feet. The western side of the basin has high tides (10 feet), but most of this coast is steep and without extensive tidal flats. North of the Spicers, however, there are large areas of shallow water (1 to 3 fathoms), extending off the islands and mainland.

Current speeds in many parts of Foxe Basin are extreme. Off Cape Dorchester, currents are reported as high as 6 knots (Putnam, 1928). Elsewhere, speeds of 2 to 4 knots are common (Campbell and Collin, MS, 1956). In several localities where current measurements have been conducted, speeds of 3.5 knots have been measured within 5 feet of the bottom.

An extensive program of bottom sampling was conducted in Foxe Basin using a Dietz–Lafond type bottom sampler. Preliminary studies of these samples have revealed that fine sediments are common in the basin. Figure 9 shows the distribution of three sediment types composed of sand, silt, and clay. The classification and nomenclature of the sediment types, sandy silt, silty sand, and clayey silt are based on the two most dominant constituents of the sediments. Fine sediments and pebbles were found together in nearly every area of the basin that was sampled. Pebble concentrations were highest south of Prince Charles Island, but in other regions of the basin, fine sediments and pebbles occurred in approximately equal concentrations.

Evidence of tidal and wave action in the shallow water zones of Foxe Basin has been observed north of Bowman Bay. Reports from aircraft describe the water as being extremely muddy, a state persisting for distances of 30 miles off the coast. In the Cape Dorchester area tidal currents and turbulence are extreme. Surface indications of a vertical movement of water have been observed and photographed on several occasions. This phenomenon is common to Foxe Basin waters and results in scouring of the bottom and lifting of fine sediments to the surface.

The development stages and formation of the dirty ice in Foxe Basin are not precisely known, but from studies of the ice, weather, and laboratory freezing experiments, a plausible account can be given. The first stage is believed to begin prior to freeze-up in September and October. During this period, a sharp deterioration of weather occurs in the eastern Arctic and there are frequent violent storms experienced in Foxe Basin. Under the influence of prolonged wind waves, the shallow inshore waters become increasingly turbid, and with each successive change of tide, the muddy water is transported further offshore. In the autumn, during the storm period, the water will attain its maximum turbidity. At this time, freezing occurs intermittently, and once it commences, the suspended sediments form an integral part of the ice.

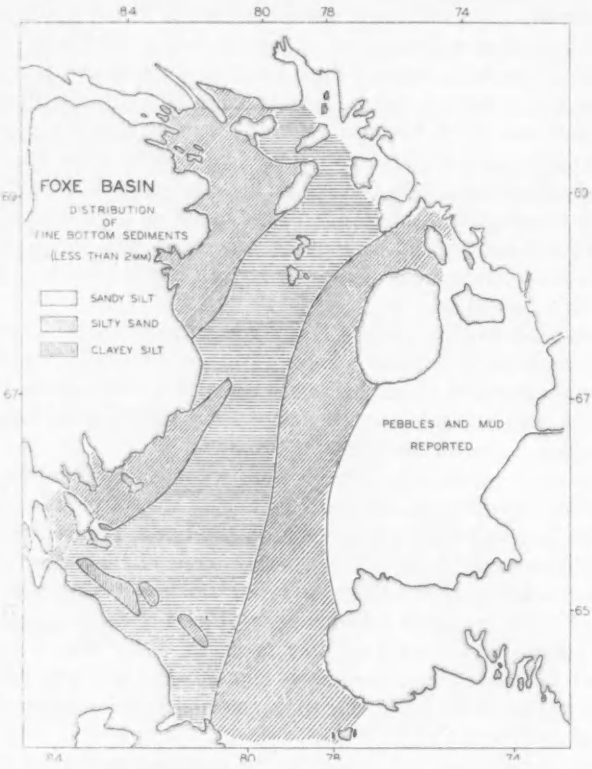


FIG. 9. Distribution of fine bottom sediments, Foxe Basin

The first type of ice to appear in agitated waters is "grease" ice or "slush" ice, and in this form the "slurry" of ice and water is capable of supporting in suspension not only the fine particles of sediment, but also coarse sand and rock fragments. Stranding of "grease" or "slush" ice on the tide flats, and subsequent movement back and forth over the bottom with each wave or change of tide, will add to the concentration of trapped sediment. Once free of the bottom, wind and tidal movement can transport the sediment-bearing ice to other regions of the basin.

When the heavier forms of ice appear, it might seem that further suspension-freezing of the sediment would end. However, other scouring actions take place with the gouging, grounding, and overturning of ice in deep and shallow water. These disturbances are largely the result of wind and tide, and so become additional agents of agitation.

The surface waters are also kept charged with sediment by powerful crushing and lifting forces exerted on the ice with the tidal decrease of the surface

area of the basin. Floes can be crushed, overturned, or made unstable until the release of pressure with the rise of tide. Consequently, pressure forces can redistribute sediments which may refreeze in ice during the winter and spring months. In all of these various ways, Foxe Basin ice acquires its two most characteristic features—sediment and uneven topography.

As soon as the ice commences to melt more dirt becomes exposed with the deterioration of the upper layers of ice and snow. Once the ice obtains this superficial sediment layer, the rate of melting increases and the ice soon acquires its stained appearance. Even in early June, this stage has reached a point when the dirty appearance of the ice is noticeable from the air. By July, the ice is extremely dirty, exhibiting its characteristic weathered appearance. Under water, the submerged ice surfaces are honeycombed, and many of the cavities contain grains of sediment. A solid blow administered by the collision of two floes, or by an ice breaker, has been observed to release such amounts of sediments into the surface water that it is impossible to see a Secchi disc a foot or two below the surface (Fig. 10).

PROPERTIES OF SEDIMENTS

Samples of dirt have been collected from Foxe Basin floes in the summers of 1955, 1956, and 1957 by H.M.C.S. *Labrador*. The quantities of dirt found in samples of ice have varied, but on the average, surface contaminants amounted to 0.5 to 2.0 g. per kilogram of ice depending on whether sampling was conducted in poorly drained areas or on the face of ice hummocks. The interior content of dirt was much less, but varied between 0.05 and 0.1 g. per kilogram of ice. With these figures, it is estimated that approximately 4 to 8 million tons of sediment become ice-borne in one yearly cycle in Foxe Basin.

Selected samples of bottom and ice sediments were forwarded to the Department of Mines and Technical Surveys, for analyses and correlation studies of the sediments. The Geological Survey Branch of that Department kindly undertook the analyses, and all references to particle size, constituents, Foraminifera, and correlations are based on their observations.

The samples referred to in Tables II and III represent selected areas of sampling in Foxe Basin. Within the four ranges of particle size (Table II), the coarse and intermediate particles are more abundant in the bottom sediments than on the ice deposits, while a far higher percentage of fine-grained particles appears in the ice sediments. This sorting would be expected if the sediment is trapped in ice through the freezing of a suspension of dirt or if the sediment is wind carried.

The differences in values in the "+20", and "20 to 80" mesh fractions of the mud samples are attributed to the abundance of shell fragments. Shell fragments were found to be more abundant in the bottom samples than the ice samples, a result which can be accounted for by the fact that shellfish are bottom living organisms.

Analyses of the coarse and intermediate particles from both the ice and bottom samples revealed, mainly, grains of quartz, biotite, schist, and limestone.

TABLE II. Size analysis of sediments.

Mesh Size	Bottom sediments				Ice sediments			
	1	2	3	Av.	1	2	3	Av.
+20	17.4	35.1	29.6	27.4	4.4	6.7	3.9	5.0
20 to 80	5.8	22.6	11.5	13.3	9.7	8.0	6.3	8.0
80 to 100	1.5	2.1	2.0	1.9	2.0	8.0	0.8	3.6
−100	75.3	40.0	57.0	57.4	84.0	77.3	89.0	83.4

20-mesh = 0.833 μ
80-mesh = 0.173 μ
100-mesh = 0.147 μ

Coarse = +20
Intermediate = 20 to 100
Fine = −100

Analyses by Department of Mines and Technical Surveys, Geological Survey of Canada Branch.

TABLE III. Modal analysis of 80–100 mesh heavy concentrates.

Minerals, etc.	3	4	6*	7*
Shells and clay particles	59.8	69.3	70.2	82.5
Quartz	35.0	25.2	24.9	10.4
Biotite	0.6	1.2	1.2	1.0
Foraminifera	0.4	0.2	...	0.5
Calcite	1.7	0.3	3.4	4.3
Garnet	0.6	2.8	...	0.3
Feldspar	1.9	1.1	0.3	...
Hornblende	...	...	...	0.5
Muscovite	...	...	...	0.5

*Specimens collected from ice floes.
Analyses by Department of Mines and Technical Surveys, Geological Survey of Canada Branch.

Accessory amounts of red feldspar, brown biotite, garnet, and hornblende were also present.

Analyses of the fine sediments are listed in Table III. The range of values for shells and clay particles, quartz, biotite, foraminifera calcite, garnet, and feldspar are wide, a result attributed to inadequate sampling or selection of samples. However, this Table demonstrates the mineralogical similarities between the bottom and floe muds, suggesting that there is a common origin.

No further evidence of the origin of the sediment can be determined from these analyses. Differences in the frosting of quartz grains were found, but no positive quantitative correlation was possible. In summary, it can be stated that the muds from the bottom and ice are derived from related sources because of the similar mineral components. The only major differences occur with the abundance of shell fragments of present-day forms in the bottom muds.

Identification of some of the biological species in the bottom muds and ice floes has revealed more conclusive results. These investigations were also undertaken by the Department of Mines and Technical Surveys.

A number of common species of Foraminifera were identified in both the mud and ice samples (Appendix). With the exception of *Fissurina marginata* and *Laryngosigma hyalascidia*, the species of Foraminifera found in the ice samples

were the same as the bottom samples. The above-mentioned species, however, have been found on the bottom in other localities in the eastern Arctic, and their absence from the few mud samples is not considered to be significant.

Fewer species were found in the ice samples and these were generally the ones that were most common in the bottom samples. All species of Foraminifera listed in the Appendix are benthonic forms.

The existence of the similar biological species in the dirty ice and the bottom sediments supports the view that the discoloured ice of Foxe Basin is of marine origin.

SUMMARY

Various factors of the origin and formation of the dirty ice in Foxe Basin are considered under two main concepts of formation: suspension-freezing of sediments and air-borne deposition of dirt.

The two theories are presented and compared in relation to a number of physical phenomena that have been observed in Foxe Basin. The facts that have been considered point to the theory of the suspension-freezing of sediments as being more complete and answering the arguments that the wind theory fails to take into account.

The analyses of the bottom sediments do not directly substantiate either theory, but reveal, mineralogically, the common origin of the ice and bottom sediments. The biological studies of the ice and bottom samples, however, show that the species of the Foraminifera found in the ice samples were benthonic forms.

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APPENDIX

IDENTIFICATION OF FORAMINIFERA

Sample #1–LAB-4 G.S.C. Loc. Cat. #32102

Composite of three samples taken at Stations 137, 138, and 139, in the area between lat. 68°00′N. to 68°03′N. and long. 79°26′W. to 80°43′W. Bottom sample.

FORAMINIFERA

? *Protoschista findens* (Parker)
Quinqueloculina agglutinata Cushman
Quinqueloculina arctica Cushman
Astacolus hyalocrulus Loeblich and Tappan
Dentalina baggi Galloway and Wissler
Dentalina frobisherensis Loeblich and Tappan
? *Laryngosigma* sp.
Elphidium bartletti Cushman
Elphidium clavatum Cushman
Elphidium frigidum Cushman
Elphidium orbiculare (Brady)
Elphidium subarcticum Cushman
Elphidium sp.
Elphidiella arctica (Parker and Jones)
Buccella frigida (Cushman)
Cassidulina islandica Nørvang
Cassidulina norcrossi Cushman
Cibicides lobatulus (Walker and Jacob)

PORIFERA

Possible sponge spicule

BRACHIOPODA

? *Hemithyris psittacea* (Gmelin)–fragments

PELECYPODA

Hiatella arctica (Linné)–fragments

CIRRIPEDIA

Balanus sp.–fragments

OSTRACODA

two unidentified genera

Sample #2–LAB-4 G.S.C. Loc. Cat. #32103

Composite of three samples from Stations 105, 108, and 112, in the area between lat. 64°16′N. to 64°31′N. and long. 79°54′W. to 81°14′W. Bottom sample.

FORAMINIFERA

? *Adercotryma glomeratum* (Brady)
Dentalina baggi Galloway and Wissler
Dentalina frobisherensis Loeblich and Tappan
Dentalina ittai Loeblich and Tappan
Elphidium clavatum Cushman
Elphidium orbiculare (Brady)
Bulimina exilis Brady
Angulogerina fluens Todd
Buccella frigida (Cushman)
Cassidulina islandica Nørvang
Cassidulina norcrossi Cushman
Cibicides lobatulus (Walker and Jacob)

DIATOMACEA

? *Coscinodiscus* sp.

Sample #3–LAB-4 G.S.C. Loc. Cat. #32104

Composite of three samples from Stations 121, 122, and 123, in the area between lat. 66°31′N. to 69°18.5′N. and long. 75°45.5′W. to 82°00′W. Bottom sample.

FORAMINIFERA

Quinqueloculina arctica Cushman
Dentalina frobisherensis Loeblich and Tappan
Elphidium bartletti Cushman
Elphidium clavatum Cushman
Elphidium orbiculare (Brady)
Elphidiella arctica (Parker and Jones)
Buccella frigida (Cushman)
Cassidulina islandica Nørvang
Cibicides lobatulus (Walker and Jacob)

BRACHIOPODA

fragments–possibly *Hemithyris psittacea* (Gmelin)

PELECYPODA

Astarte sp.
one unidentifiable specimen } fragments

CIRRIPEDIA
Balanus sp.
OSTRACODA
Cyprideis sorbyana (Jones)
Cytheridea punctillata (Brady)
Cytherura clathrata Sars
? *Cytheropteron* sp.
Xestoleberis aurantia Baird
one ostracod indeterminable.

Sample #6–LAB-4 G.S.C. Loc. Cat. #32105
South Foxe Basin. Sample from melt water pool on ice surface.
FORAMINIFERA
Elphidium bartletti Cushman
Elphidium clavatum Cushman
Elphidium orbiculare (Brady)
Buccella frigida (Cushman)
Cibicides lobatulus (Walker and Jacob)
OSTRACODA
Xestoleberis aurantia Baird

Sample #7–LAB-4 G.S.C. Loc. Cat. #32106
South Foxe Basin. Sample from surface layer of ice.
FORAMINIFERA
Fissurina marginata (Montagu)
Laryngosigma hyalascidia Loeblich and Tappan
Elphidium bartletti Cushman
Elphidium clavatum Cushman
Elphidium orbiculare (Brady)
Elphidium subarcticum Cushman
Angulogerina fluens Todd
Buccella frigida (Cushman)
Cassidulina islandica Nørvang
Cassidulina norcrossi Cushman
Cibicides lobatulus (Walker and Jacob)
OSTRACODA
Cytheropteron sp.

Sample #8–LAB-4 G.S.C. Loc. Cat. #32107
South Foxe Basin. Sample from surface layer of ice.
FORAMINIFERA
Fissurina marginata (Montagu)
Elphidium clavatum Cushman
Elphidium orbiculare (Brady)
Cibicides lobatulus (Walker and Jacob)

Effects of High Temperature on Survival of the Giant Scallop[1]

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ABSTRACT

Upper lethal temperatures of scallops are raised 1°C. by each increase of 5°C. in acclimation temperature. Acclimation upwards is fairly rapid (average 1.7°C. per day over part of the range). Loss of acclimation to high temperature is slow, and appears to take as long as 3 months. There is a winter-to-summer *decline* in lethal temperature. It appears that naturally occurring water temperatures over 23.5°C. will be lethal to scallops and directly responsible for mortalities. Temperatures over 21°C. may also be a direct cause of mortalities but only in special circumstances could mortalities occur as a direct result of temperatures below this. In the "sub-lethal" temperature range, sudden temperature changes upward or downward may so reduce scallop mobility as to make them easier prey to enemies. In this way sudden temperature change could be an indirect cause of increased mortality.

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INTRODUCTION

Sudden mass mortalities among populations of the giant scallop, *Placopecten magellanicus* (Gmelin), have been observed in the southwestern Gulf of St. Lawrence from time to time since 1928. They may result from sporadic intrusions of unusually warm water onto the scallop beds. However, there is no published information on the scallop's ability to withstand high temperatures. Without such information it is impossible to say whether these mortalities are the direct result of lethal effects of high temperature, or an indirect result mediated through starvation, depredation or disease organisms.

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The primary purpose of the work reported here was to describe the direct effects of high temperature on scallop survival, according to concepts and methods outlined by Fry (1947). At the same time we report observations of changes in behaviour which resulted from temperature change. The changes in behaviour seem likely to have indirect effects on survival through their influence on the scallop's ability to escape predators.

ACKNOWLEDGMENTS

During these experiments the writer has been associated with several other investigators. Most of the earlier work was carried out at the Fisheries Research Board's St. Andrews Biological Station by Dr. L. P. Chiasson of the Department of Zoology, St. Francis Xavier University, after consultations and advice from Dr. J. C. Medcof, Dr. D. W. McLeese and the writer. Dr. Chiasson was assisted by Mrs. E. I. Lord and Mr. J. S. MacPhail, who with Dr. Medcof and the writer carried out several of the earlier winter experiments as well as the late 1956 and all the 1957 experiments. The early 1956 tests were carried out under direction from the writer by Mr. R. E. Johannes assisted by Mrs. Lord and using equipment set up by Mr. A. W. Holt.

I wish to express my pleasure at having been associated with these people, and to thank all who have assisted with the program. I particularly appreciate the advice of Dr. Medcof and Dr. McLeese during various phases of the work and thank them for criticisms during interpretation of results, and preparation of the manuscript.

MATERIALS AND METHODS

History of Experiments

Experiments described here were begun in July 1952 and continued through December 1957. Because of the length of time involved a number of different investigators took part in the work. Care was therefore necessary to avoid errors which might be introduced on this account alone. This was achieved by having the same person associated with critical parts of all the experiments.

During the work, improvements were made in the equipment for maintaining constant temperatures and water flows. From 1952 to 1954 apparatus used was similar to that described by McLeese (1956). However it limited the number of tests which could be made at any one time, and in 1956 and 1957, with advice from Dr. McLeese, it was modified to permit more elaborate experimental designs. Throughout the experiments, standards of space for holding, acclimation and lethal testing were maintained at levels found to be satisfactory in the pilot tests.

Stocks and Initial Handling

Scallops used for the majority of the experiments were fished from the Mascarene shore bed at 40 fathoms (73 m.) in southeast Passamaquoddy Bay. They were fished with commercial inshore-type scallop gear (MacPhail, 1954) and placed in a large tank on the boat deck. A rapid flow of salt water was

maintained through the tank until the animals could be landed at the Biological Station, usually about 2 hours after fishing began. There they were culled for broken hinges or other injuries, the shells cleaned of epifauna and detritus, and about 3 hours after being fished they were placed in holding tanks described below. They were frequently held in these tanks at ambient temperatures (in sea water pumped directly from Brandy Cove, the site of the Biological Station) for a day or two before some of them were transferred to acclimation tanks. A control lot was kept at the initial holding temperature. In spite of careful treatment, cull of animals injured during fishing and handling was usually between 10% and 15% of the initial catch.

On one occasion in 1956 a sample of scallops was fished from 45 fathoms (82 m.) in the Digby area of the Bay of Fundy and carried in tanks by boat to the Biological Station, a distance of about 60 miles. They were placed in holding tanks at St. Andrews about 8 hours after being fished. There were no apparent ill effects of the more rigorous treatment.

On July 7 and 23, 1956, scallop samples were fished from the Toney River bed in Northumberland Strait (southwestern Gulf of St. Lawrence) off Pictou, Nova Scotia. They were landed near Pictou about 2 hours after being fished and carried by truck to St. Andrews, a distance of about 300 miles. During transportation they were held in moistened insulated boxes at about 2°C. Delivery to the holding tanks took place about 15 hours after fishing. During holding and acclimation there was a 5% mortality of the first sample and a 20% mortality of the second.

Holding and Acclimation

Wooden tanks, measuring 3 × 3 × 2½ feet, or of comparable size, painted inside with white Tygon plastic paint, were used for holding, for acclimations and for controls. In early experiments the necessary heated sea water was supplied from a reservoir through a series of 400 watt, glass-lined heaters. Tank temperatures were maintained by thermostatic control of the heaters, combined with regulation of the rate of flow. In 1957 water was heated to a high temperature in a furnace and mixed with appropriate flows of cold water, to produce desired tank temperatures. Air from a compressor was delivered through air stones fixed at the bottom of the tanks and tests showed that it kept the water saturated with oxygen. The bubbling also kept the tank water thoroughly mixed and prevented thermal stratification.

Cold water temperatures for work during summer were obtained by refrigeration of the sea water in the large wooden or glass tanks. It was impractical to use flowing refrigerated water. As with other tanks the water was kept saturated with oxygen. Scallops placed in these tanks survived as well as those in other holding and acclimation tanks.

As many as 150 scallops were kept in the holding tanks at ambient temperatures for periods of from a week to 3 months, depending on the experimental design. Similar tanks were used subsequently for acclimating the samples to higher or lower temperatures for periods of a week to a month. They were

examined frequently, and records were kept of water conditions, and of animals that died. Dead animals were removed.

In most cases there were no apparent ill effects of the initial holding or acclimation treatment but in a few cases there were excessively high mortalities. These were almost always traced to failures in the water-flow, air-flow or temperature controls. Except for one lot of scallops fished from the Gulf of St. Lawrence on July 23, 1956, all samples which showed more than 5% mortality during holding or acclimation were discarded as possibly no longer representative of natural populations.

With few exceptions acclimation temperatures were maintained within $\pm 1.0°C.$ of the intended temperature. Generally 3 acclimation temperatures were used; at about 5, 10 and 15°C. In later experiments some tests were performed with scallops acclimated at 20°C., and one winter test was carried out with scallops subjected to –1.5°C.

During lethal tests control lots of scallops were retained in the acclimation tanks, and at no time did mortalities occur among them.

Lethal Tanks and Tests

Lethal temperature tests were performed in unpainted wooden tanks measuring 2 ft. $\times$ 2 ft. $\times$ 6 in. In early experiments the method of heating sea water was the same as that described for the holding and acclimation tanks, and it was difficult to keep temperatures in them within $\pm 0.5°C.$ of that intended. In 1956 and 1957 sea water flowing from overhead constant-level tanks was fed to upright heating tanks containing thermostatically controlled heaters. Water close to the temperatures required for lethal tests was taken from the appropriate levels in these tanks and, by adjusting the flow, it was possible to maintain test temperatures to within $\pm 0.4°C.$ Water in lethal test tanks was kept mixed and saturated with oxygen by bubbling air through air stones in the bottom of the tanks.

Scallops were transferred directly from acclimation tanks to lethal test tanks. In experiments comparing "large" and "small" scallops, 10 of each of the 2 size categories were placed in each test tank. The same procedure was followed in tests comparing local and Gulf of St. Lawrence stocks. In all other cases 10 scallops were used per test tank.

Experiments lasted from 24 to 120 hours and observations were made once each hour. At each observation dead scallops were removed, measured, their sex determined, and any necessary temperature adjustments made. At the end of the experiments the condition of survivors was recorded, and unless required for other reasons they were discarded.

Definition of Lethal Temperature

Fry (1947) defines the upper incipient lethal temperature as that temperature above which 50% of the population cannot live indefinitely. Below this is a *zone of thermal tolerance*, and above it, a *zone of thermal resistance* (Fry, Hart and Walker, 1946). Fry (1947) and others have shown that for fish acclimated

to a given temperature, the logarithm of survival time in the zone of thermal resistance is related linearly to temperature, indicating that the mechanism responsible for thermal death is constant throughout the zone (Brett, 1956). However, Chiasson (MS, 1954) found indications of a decrease in rate of survival of scallops after 48 hours. This was taken to mean that after 48 hours the factors responsible for scallop death had changed, and that it may no longer have resulted from temperature alone. He therefore defined the upper incipient lethal temperature for scallops as that temperature above which 50% of scallops could not live for 48 hours.

During 1956, Johannes (MS, 1957) repeated Chaisson's experiments but failed to confirm any change in survival rates at high temperatures for periods of up to 120 hours. For periods longer than 120 hours survival rate in the lethal test tanks was high and indistinguishable from survival rate in the holding and acclimation tanks. No explanation for Chaisson's earlier observation has been found, although during 1956 several 120-hour lethal temperature tests were performed. The 48-hour period was, however, maintained as a standard lethal test procedure.

Chiasson's preliminary experiments showed that scallops will be killed in 48 hours by a temperature between 20 and 27°C. To determine the upper lethal temperature, 4 testing temperatures at 1°C. intervals within this range were selected such that little or no mortality occurred at the lowest and about 100% at the highest. Ten scallops from each acclimation temperature were subjected to each of the 4 test temperatures. The temperature required to kill 50% of the 40 animals in 48 hours was then interpolated from the results.

It has been repeatedly shown (Fry, Brett and Clawson, 1942; Brett, 1944; and others) that the upper lethal temperature for many species may be progressively increased by increasing the acclimation temperature. That is, the upper lethal temperature appears as a line of positive slope when plotted against acclimation temperature. Three levels of acclimation temperatures were used in the 1956 and 1957 tests to establish the slope and position of this line.

Determination of Death

A scallop was considered dead if the velum failed to contract when stimulated by a glass rod. The reaction is relatively easy to detect, and no scallops which lost velar contractility ever recovered when replaced in water of their former acclimation temperature. This criterion for death was chosen by Chiasson during the early experiments as more reliable than alternatives such as lack of shell or tentacular movement, or separation of the velum from the valve; reactions which occurred in animals later classed as "dead". Comparisons among determinations by different workers showed that their opinions as to time of death rarely differed by more than 1 hour when this criterion was used. In no case was there difficulty in classifying animals as "living" or "dead" at the end of a test.

Although easy to apply, it is certain that the criterion "loss of velar response" is an excessively severe test for scallop death. That is, the point of breakdown

of organization of the animal, beyond which there is no recovery with amelioration of environment, occurs before complete loss of velar response. Experience with holding survivors from the test showed that those classed as "weak" at the end of a test were likely to die in periods of a day to a week following their replacement in sub-lethal temperatures, while "vigorous" animals survived as well as the controls. Therefore, in the late 1956 and all the 1957 tests, survivors were classified according to condition in order to appraise "over-severity" of the criterion and to assess differences in apparent and true lethal temperatures.

RESULTS

Relation of Lethal Temperature to Acclimation Temperature

Results from test begun on February 6, 1957, are given in Fig. 1, and are typical of those obtained in all experiments. Similar illustrations have been given for lobsters by McLeese (1956) and for scallops, from the 1956 experiments, by Johannes (MS, 1957). In the February 1957 experiments, temperatures during acclimation averaged 5.2°C., 10.5°C. and 15.5°C. The 4 test temperatures were 22 to 25°C. for scallops acclimated at 5.2 and 10.5°C., and 23 to 26°C. for those acclimated to 15.5°C. These ranges satisfied the requirement of no mortality at the lowest test temperature and complete mortality at the highest except for the lots acclimated at 5.2°C. In these the mortality was 40% at 22°C., the lowest

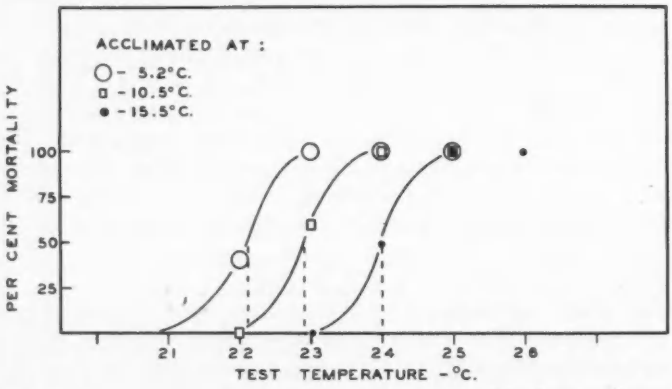

Fig. 1. Percentage mortality in 48 hours of sample lots of scallops acclimated at 5.2, 10.5 and 15.5°C. and subjected to various higher test temperatures.

test temperature. It seems justifiable on the basis of the other results to conclude that mortality for this lot would have been close to zero at a test temperature of 21°C. and the results have been interpreted accordingly. From the sigmoid curves drawn through the mortality data in Fig. 1, it is judged that the temperature required to kill 50% of scallops acclimated at 5.2, 10.5 and 15.5°C., was 22.1, 22.9 and 24°C. respectively.

The regression of these 48-hour, upper lethal temperatures on acclimation temperatures is given in the upper line of Fig. 2. Other experiments using acclimations as low as 2.5°C. and as high as 20°C. have been performed on scallops collected during winter and spring. The results confirm that lethal temperature is raised by acclimation to higher temperatures throughout the temperature range examined, and probably justify the extension of the line in the manner shown. In such a case points of intersection of the line with the ordinate at the freezing point of sea water and with the diagonal marking the locus of points where acclimation and lethal temperatures are the same,

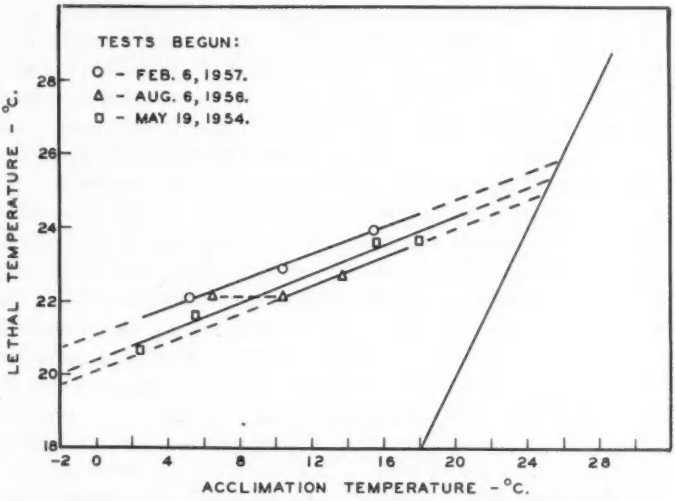

FIG. 2. 48-hour upper lethal temperatures for scallops, as shown by tests on 3 different dates. The solid diagonal on the right side of the figure is a construction line marking the locus of points where acclimation temperatures are the same as lethal temperatures.

correspond with Fry's (1947) minimum and ultimate upper incipient lethal temperatures for experiments continued for an "indefinite" time. Because these scallop tests were restricted to 48 hours, the terms "minimum" and "maximum" upper lethals (cf. McLeese, 1956) are more appropriate than Fry's. They are, respectively, 20.8°C. and 25.8°C.

At the 10°C. temperature to which scallops are frequently exposed in nature, and at which they appear to grow most vigorously (Posgay, 1953) and spawn successfully (Dickie, 1955), the 48-hour upper lethal is at 23.0°C.

The slope of the line in Fig. 2 indicates that a rise or fall of about 5.0°C. in acclimation temperature produces a corresponding change of 1.0°C. in lethal temperature. This rate of change lies in about the middle of the range of values found for other species. In the young goldfish, *Carassius auratus*, a rise of only

3°C. in acclimation temperature results in a 1°C. rise in lethal temperature (Fry, Brett and Clawson, 1942), whereas a 7°C. rise in acclimation temperature is required to produce the same change in lethal temperature of the speckled trout, *Salvelinus fontinalis* (Fry, Hart and Walker, 1946).

Rate of Acclimation to Higher Temperatures

The relationship illustrated by the February 1957 test in Fig. 2, top line, requires the assumption that the scallops were fully acclimated to 5.2, 10.5 and 15.5°C. They had been collected on January 9, 1957, from water of 3.7°C., and handled in standard fashion at low temperatures before being placed in the acclimation tanks on January 10, 28 days before the lethal tests. The validity of the assumption of complete acclimation is supported by results of a special series of tests by Chiasson, together with results of the recent tests. It is also supported by obervations of the behaviour of scallops reported in a later section.

Chiasson (MS, 1952) performed a series of experiments to determine speed of acclimation when the ambient temperature was raised abruptly from 10°C. to 15°C. He performed lethal tests on samples of animals withdrawn at regular intervals from the acclimation tank and found no appreciable difference in lethal temperatures or resistance times of successive lots after about 3 days of acclimation. He concluded that acclimation had been completed in this time. The average rate of acclimation to the higher temperature was 1.7°C. per day.

Except in one instance, scallops used in all lethal test experiments described in this paper were retained in acclimation tanks for periods of between 1 and 4 weeks, long enough to permit acclimation to higher temperatures if it proceeded at a rate only half that observed by Chiasson. The longer acclimation periods were used in winter and spring when sea temperatures at time of collection were lowest (between 2.5 and 4.8°C.), and the shorter periods of 1 to 2 weeks were used in summer and autumn when sea temperatures were highest (9 to 12°C.). The one exceptional test was conducted on August 6, 1956, after an acclimation time of only 4 days from collection at a temperature of 9.0°C. Results from this test are given in the lowest line of Fig. 2. The slope of that part of the line involving acclimation temperatures above 10°C. is the same as that for the February 6, 1957 test involving acclimation for 28 days, and the same as that for all similar tests during 1956 and 1957. It seems safe to conclude that in every case acclimation to increased temperatures was complete before lethal tests were undertaken.

Loss of Acclimation to Higher Temperatures

Loss of acclimation to high temperature takes place exceedingly slowly. This phenomenon has been observed among fishes (Brett, 1956) and is illustrated for scallops by tests carried out in late 1957. Scallops were collected on October 31 from a temperature of 9.9°C. and transferred to holding tanks at St. Andrews where temperatures were fluctuating between 9 and 11.5°C. On November 2 a number of these were placed in colder water fluctuating in temperature between 3.5 and 6.5°C., and held there. The remainder were kept

in the holding tank until November 20 when they were divided into four lots. One was left in the holding tank for a control. The other three were put in acclimation tanks—one at 3.5 to 6.5°C. (colder than the holding tank), one at 13.0 and one at 18.5°C. Lethal temperature tests were performed on December 12 using scallops first subjected to low temperatures on November 2, as well as samples of those acclimated at 13.0 and 18.5°C. Further tests were performed on December 16 using scallops placed in the 3 acclimation tanks on November 20. The results in Fig. 3 show that although one lot had been subjected to low

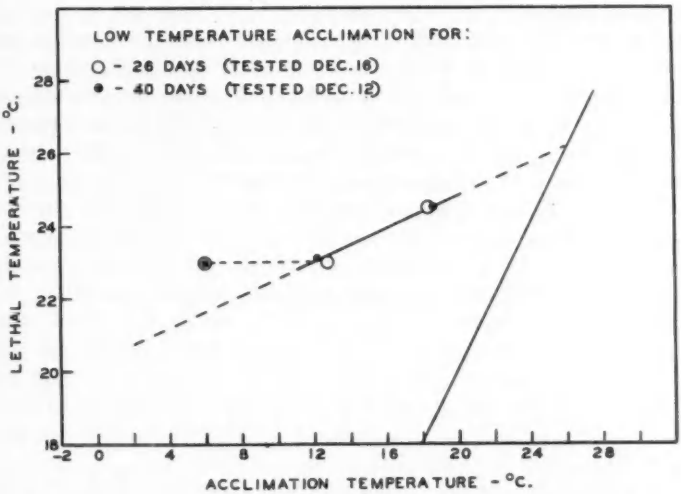

FIG. 3. 48-hour upper lethal temperatures recorded in 2 experiments in December, 1957, with scallops "acclimated" at 3 temperatures. The 6°C. acclimation period was 40 days in the first experiment and 26 days in the second. A construction line like that of Fig. 2 is drawn on the right.

temperature for 26 days and another for 40 days, their lethal temperatures were identical. Furthermore the lethal temperature of all these "cold-acclimated" scallops was the same as would have been expected for scallops acclimated to about 12.0°C. We can conclude only that the scallops had failed to reduce their high-temperature acclimation to that characteristic of 3.5 to 6.5°C. temperatures even after 40 days' exposure. Apparently they were still in a state of acclimation to the high temperatures they encountered either earlier in the season while they were still on their beds, or during the initial handling and holding phases of the experiment.

The hypothesis that scallops lose their acclimation to higher temperatures very slowly, or at least that they fail to adjust their state of acclimation to that characteristic of temperatures lower than that to which they have been recently exposed, explains an anomaly of the incipient upper lethal temperature lines

obtained in all summer experiments. It is illustrated by the lowest line of Fig. 2, taken from the August 6, 1956 test. The slope of this line based on the higher acclimations is virtually the same as for the February 1957 tests indicating complete acclimation at these levels, but scallops held at 6.5°C. for acclimation reacted as though they were acclimated to 10°C. This is 1°C. higher than the temperature of the water at the time they were collected for the experiments and a temperature to which they may have been exposed for appreciable lengths of time during handling and holding. It is reasonable to conclude that although acclimation to increased temperatures is relatively rapid, the loss of high-temperature acclimation is extremely slow.

As far as data are available, they show that loss of acclimation to high temperatures takes place as slowly in nature as it did in the tanks. This is illustrated by results of tests begun on October 2, 1956, and on November 7, 1956. The scallops used were collected from water of 10.8°C. on September 25 and of 9.9°C. on October 23, respectively, and had lethal temperatures very like those of August 1956 when only acclimation temperatures of 11°C. and over are considered. However, the scallops exposed to water of 6°C. for 7 and 15 days respectively, acted in each case as though they had been acclimated to water of 11°C., about the maximum temperature of the water during late summer. Although our records of handling are not complete enough to rule out inadvertent exposure to water as warm as 11°C. during the initial collecting, handling and holding phases, it at least seems unlikely that the lot collected on October 23 was so exposed. The concurrence of the "11°C.-lethal" in scallops subjected to colder water, and the 10.8°C. temperature in late September therefore strongly suggests retention of a state of acclimation to late summer conditions up to early November at least.

The next seasonal collection following the tests of November 7, 1956 was that made in January, 1957 for the February tests, at which time the lethal for 5.0°C. acclimations falls onto the line with those for higher acclimations (Fig. 2, top line) suggesting that acclimation to the lower temperature was complete. However, because in this case the position of the whole line is high compared with the summer line, better assurance of acclimation to lower temperatures is afforded by comparing results of the August 6 test with those of a test performed in May, 1954. The scallops for the latter experiment were collected on January 27, 1954, when the water temperature was about 5.6°C. They were held at temperatures lower than this for several weeks until acclimations were begun at approximately 2.5, 4.5, 15.5 and 18.0°C. The resulting 48-hour lethal temperatures have been marked on Fig. 2 and fall along a line just above and parallel to that fitted to the August 6 data, but provide points at both upper and lower acclimation temperatures beyond those available from the August 1956 tests. The February 1957 and May 1954 data show that acclimation (in respect to high-temperature resistance) to temperatures as low as 5.5 and 2.5°C., respectively, had taken place during the winter months.

We must conclude that scallops lose their state of acclimation to high temperatures very slowly. Inadvertent exposure to high temperatures during

initial handling does not appear as a factor determining the lowest level of temperature to which the scallops could be acclimated in at least one experiment. The data suggest rather that scallops collected in November may still retain their state of acclimation to near the maximum seasonal temperatures of late September or early October. Scallops collected in January appear to have lost their acclimation to high temperature. It appears, therefore, that loss of acclimation to high temperature may take as long as 3 months.

Changes in Behaviour following a Rise or Fall in Temperature

Changes in the behaviour of scallops support the conclusion from the foregoing sections that the animals adjust rapidly to rising temperatures, but slowly to falling temperatures.

Scallops of 80 to 100 mm. shell diameter held in normal temperatures lie on their right side with valves of the shell gaping about 15 to 30 mm. Their tentacles are extended and the velum "raised" in the form of a curtain closing off the mantle cavity except at the ventral and dorsal margins where there remain slit-like openings serving as incurrent and excurrent passages for water. Scallops in such a position respond to slight changes in illumination, to shadows, or to prodding with a glass rod by a sudden closure of the valves. They will react to disturbances such as tapping on the walls of the tank, by active swimming.

When placed into water warmer than acclimation conditions by about 10°C., they generally became insensitive to stimulation and in all cases when they were placed in water above about 20°C., they became sluggish and generally produced large quantities of mucus. However, when the test temperature was sub-lethal they stopped producing mucus after 12 hours and by 36 to 48 hours acted in apparently normal fashion. The rapidity of this return to normal behaviour accords with Chiasson's conclusion that physiological adjustment to increasing temperature is rapid.

When scallops were taken from water of 10 to 12°C. in late summer or autumn, and subjected to temperatures between 3.5 and 6.5°C. for acclimation they closed the valves of their shells to within 5 mm. of each other and remained in this position with the mantle space completely curtained off by the velum and with the tentacles only slightly extended, for periods as long as 40 days. They responded to persistent prodding by closing their shells more tightly, but did not react to changes in illumination nor could they be made to swim by tapping on the tank. When removed from the water they responded by slow but strong clapping of the valves. Their reactions became normal a few hours after their return to warm water.

Deaths of scallops suddenly subjected to cold water were rare, even in the prolonged acclimation periods, indicating no immediate deleterious effects of the treatment. But their behaviour in the cold is in striking contrast to the sensitivity to stimuli and the vigorous reactions of scallops collected in winter and spring from water temperatures as low as 2.5°C. It is apparent that, although scallops can live and react normally in water temperatures as low as 2.5°C., they

are extremely slow to adjust to these conditions when placed in them directly from temperatures of 9 to 12°C. In the experiments described earlier any drop of 4 to 7°C. in ambient temperature was enough to cause virtual immobility for prolonged periods.

While not affecting survival directly, these responses to a sudden rise or fall in temperatures may have an important indirect bearing on survival in the natural environment.

Influence of Reduced Oxygen Supply during Acclimations

On two occasions during 1956 experiments, the air supply was accidently turned off during acclimations. Johannes (MS, 1957) reports that in each case the animals were gaping when the fault was discovered, but, recovered their normal reactions within a few hours after the air supply was renewed. The reductions in oxygen level were not measured, but reactions of the scallops were similar to those noticed by van Dam (1954) in water poor in oxygen (less than 1 cc. 0_2/l.). Johannes used the scallops so affected on June 17 in a lethal temperature experiment beginning on June 18. He found that compared with animals from the same acclimation lots tested 4 days previously, the lethal temperatures had fallen 0.5°C. for those acclimated to 15°C. and 0.9°C. for those acclimated to 7°C.

Brett (1944) found that low oxygen tension inhibited temperature acclimation in the bullhead, *Ameiurus nebulosus*, and McLeese (1956) showed that lowering the oxygen supply during acclimation lowers the lethal temperature of the lobster, *Homarus americanus*. In both these investigations, oxygen supply was kept low during the entire acclimation periods. In the case of the accidents with scallops, however, the water had been saturated with oxygen long enough to permit full temperature acclimation. The lowering of lethal temperature following temporary exposure to low oxygen therefore indicates that the effects of acclimation on toleration of high temperature had been reversed.

The results show the importance of maintaining a sufficient air supply to the tanks during lethal temperature tests. The relationship was, however, not studied further because low oxygen tension does not seem likely to occur in the natural environment of scallop beds.

Influence of Reduced Salinity during Lethal Temperature Tests

Scallops are normally inhabitants of open water, where they rarely encounter salinities much below 30‰. However, temperature changes in the Gulf of St. Lawrence are known to be accompanied by changes in salinity of the order of 1.5‰ to a low of 27‰ at some seasons (Lauzier, 1952). Accordingly Johannes conducted experiments to examine the effects of reduction of salinities of water used in the lethal temperature tests from 30‰ to 25‰ and 20‰. The scallops had been acclimated under normal salinities (30‰ or over). He found that lowering salinity to 25‰ had little appreciable effect on temperature tolerance, although a salinity of 20‰ depressed the lethal temperature by about 1°C. for scallops acclimated to temperatures between 7 and 16°C. Salinity changes, therefore,

seem unlikely to affect the ability of scallops living in open water to withstand high temperature, although they may influence survival in some shallow-water, shore areas.

Seasonal Changes in Heat Tolerance

The difference in positions of incipient upper lethal lines for February and August tests (Fig. 2) is representative of differences encountered among lethal temperature experiments at different seasons of the year, and suggests that there

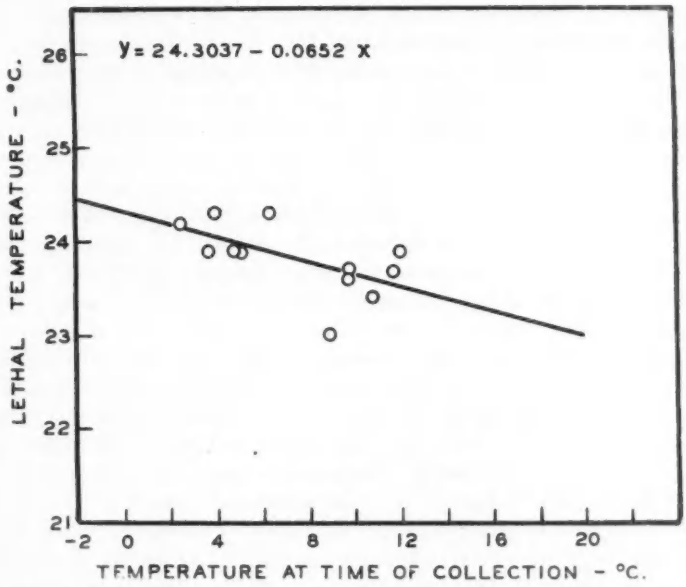

Fig. 4. Relation between 48-hour upper lethal temperatures for Passamaquoddy Bay scallops acclimated to 15°C., and the water temperature when they were collected.

is a seasonal difference in tolerance of high temperatures. Comparisons of upper lethal temperatures cannot be made for all acclimation temperatures because of the impossibility of acclimating scallops in a reasonable time to temperatures below that at which they were collected. However, in each test, part of the scallop sample was acclimated to a temperature of about 15°C. which is higher than the normal maximum seasonal temperature in the vicinity of the scallop beds. Fig. 4 shows the relation between 48-hour upper lethal temperatures of scallops acclimated to 15°C. and the temperature of the water on the beds at the time they were collected, for all collections made in 1956 and 1957. Scallops fished from cold water during winter and spring appear able to tolerate higher temperatures than those fished during the warmer summer and autumn months.

Some caution must be exercised in interpreting these data. Fig. 4 uses all the 1956 and 1957 experimental results and the resulting negative slope seems sufficiently reliably determined (95% confidence limits of the slope are —0.028 and —0.128). However, in calculating the line we have excluded results obtained from tests prior to 1956. Scallops from the test begun on May 19, 1954, were collected on January 27 at a temperature of about 5.6°C. When tested nearly 4 months later, after acclimation of about a month, their lethal temperature was 23.2°C., only slightly above the result for the summer test of August 6, 1956. This point was excluded partly on the basis of the long and possibly debilitating holding period, but primarily because it seems to be related more closely to results of tests in March 1953 and July 1952 than to later work. In these two early experiments lethal temperatures for 15°C. acclimations were about 23.8 and 22.3°C. respectively. If reliable, they form a series with the May, 1954, test similar to that shown by the 1956 and 1957 data, but on a lower level of temperature tolerance. None of the data for these two tests have, however, been included in Fig. 4 as detailed records of temperature at time of collection and methods of handling and acclimations are not available and the slopes of the lethal lines derived from them are different than from those done later (Fig. 2). Should they be directly comparable they not only confirm seasonal differences, but suggest, in addition, that there may be some year-to-year differences in temperature tolerance.

Seasonal changes in heat tolerance among some freshwater fishes were reported by Brett (1944) and Hart (1952) who showed that they resulted from acclimation to seasonal changes in their environmental temperature. If this were the explanation for the phenomenon observed in scallops, one would expect heat tolerance to be lower in winter than in summer, whereas the reverse is true. There is no apparent relation between these results and variations in salinity and oxygen during the tests. It appears that the seasonal change is related to temperature experience in some way which is not directly related to "acclimation" in the sense we have considered it up to now, and may to some extent actually reverse the effects of this process.

Seasonal variations in lethal temperatures have not been reported for other species but it would not be surprising if they do occur. Hoar (1955) showed that goldfish which had been held at a standard temperature for a long period survived in lethally warm water for a longer time in summer than in winter, and survived in lethally cold water longer in winter than in summer. The differences appeared to be independent of the previous holding temperature, and were attributed to changes in physiological state related to endocrine activity.

Seasonal variations in sensitivity of the frog, *Rana pipiens*, to hormone injections have been noted by Biesinger and Miller (1952). Hall, Fisher and Stern (1954) have reported marked differences in the sensitivity of isolated frog muscle (*R. pipiens*) to insulin or citrate in summer and winter, though the control rate of oxygen consumption was very little different in the two seasons. Sullivan and Fisher (1953) demonstrated that from autumn to spring there are marked differences in the temperatures selected from a gradient by speckled

trout, *Salvelinus fontinalis*, and showed that the difference is at least partly independent of acclimation temperature. Bennett (1954) reports a seasonal change in the rhythmic activity of the quahog, *Mercenaria mercenaria*, held under constant conditions. Seasonal changes in water and glycogen content of the flesh of molluscan shellfish such as oysters are well known (Medcof and Needler, 1941) and changes in condition related to the spawning cycle of many marine animals are common knowledge.

It seems likely that seasonal differences in lethal temperature for scallops are real and reflect seasonal differences in physiological state of the animals, in addition to those determined by their immediate past temperature experience. Further work may demonstrate similar dependence of lethal temperatures of other species on their physiological state. However, the complexity of the dependence of physiological state on seasonal changes in environment (Hoar, 1957) may often obscure this dependence more than seems to have been the case with scallops.

Relation between Lethal Temperature and Test Duration

The 48-hour period used to determine lethal temperature in these experiments does not appear to measure the true incipient upper lethal temperature. It was pointed out above that early experiments indicated that factors other than temperature alone may affect scallop survival in lethal test periods longer than this. When Johannes failed to confirm this hypothesis, the 48-hour test period was retained as a matter of convenience, although several comparisons were made of lethal temperatures measured by the 48-hour and 120-hour tests. These indicate that the 120-hour period gives estimates of lethal temperatures 0.8°C. (range, 0.6–1.0°C.) lower than those discovered in the 48-hour period. That is, for any acclimation temperature, 50% of scallops will be killed in 120 hours (5 days) by temperatures about 0.8°C. lower than temperatures which kill this many in 48 hours (2 days).

Relation between Measurements of Lethal Temperatures and Determination of Death

It has been pointed out that although loss of velar response is a dependable criterion for measuring the relative resistance of scallops to high temperature, it is a servere criterion of death. This is illustrated by Fig. 5, taken from a 48-hour lethal temperature test begun on April 29, 1957. The data show that if scallops which appear "weak" (dying) at the end of the experiment are added to those which were dead (lacked velar response) then the corresponding upper incipient lethal temperature will be 0.5°C. lower than that which emerges when loss of velar response alone is taken as the criterion of death.

This lower temperature must be regarded as a more faithful estimate of the upper incipient lethal temperature even though the personal error in applying the semi-qualitative criterion "weak", versus "normal" or "vigorous" leads to variation in the amount of apparent lowering in the lethal temperature from experiment to experiment, or even among acclimation lots of the same experiment.

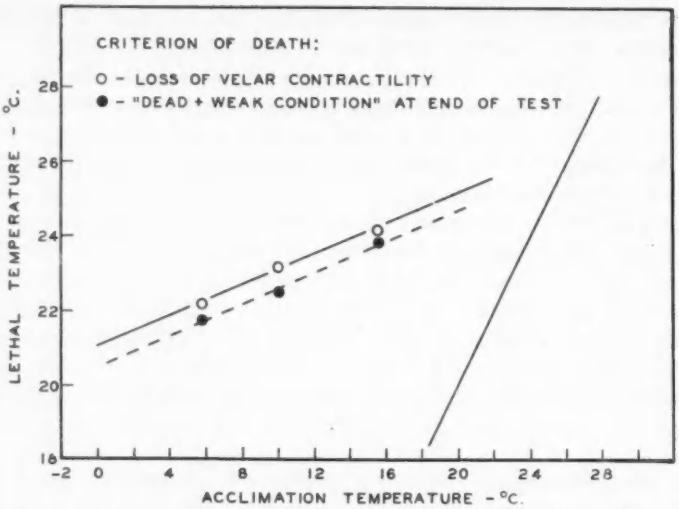

FIG. 5. Differences in estimated upper lethal temperatures when different criteria for death are applied to records from a 48-hour test begun on April 29, 1957. (Construction line as in Fig. 2.)

The drop of 0.5°C. in Fig. 5 is about average, the range from all experiments being 0.2 to 0.7°C. Furthermore the difference in amount of drop at different acclimation temperatures within any one experiment was about average. In this example it ranged from 0.3°C. at 15.5°C. to 0.6°C. at 10°C. Poorest internal consistency of any test was shown by that begun November 7, 1956. The lethal temperature drop was 0°C. at an acclimation temperature of 15.5°C. but 0.7°C. at an acclimation temperature of 5.3°C.

Data for comparing paired estimates of the upper incipient lethal temperature derived from 120-hour and 48-hour lethal test periods are available for only one experiment, that of August 6, 1956 (Fig. 2). In this experiment when loss of velar response alone was used the 120-hour upper lethals were 0.6°C. lower than the 48-hour upper lethals. When weakened animals as well as those that had lost velar response were counted as dead, the 48-hour lethal was lowered more than the 120-hour lethal. As a result the two were identical for the highest acclimation temperature and the 48-hour estimate was only 0.3°C. lower than the 120-hour for the two lower acclimation temperatures.

This small difference between the estimates of the lethal temperature when different criteria for "dead" scallops are applied to records of 120-hour lethal tests supports Johannes' statement that rate of survival after 120 test hours was not appreciably different from that in the control tanks. We must conclude that most animals which will be killed by any high temperatures will show signs of weakening within the first 48 hours of exposure. However, a small proportion will not show effects until 5 days after exposure and will not appear "dead" until

after this. The velar response is therefore a too-severe criterion of death even in long test periods, and for any acclimation temperature the true upper lethal temperature is probably uniformly 0.2 to 0.3°C. lower than that derived from the 120-hour lethal tests using loss of velar response as a death criterion.

Temperatures Lethal to 25%, 50% and 75% of Scallop Samples

When comparing one set of lethal temperatures with another, it is most convenient to use 50% mortality points, taking into account the scatter about this average as a measure of the relative accuracy of the measurement. However, in field observations we may encounter smaller mortalities which affect the population so little that they almost escape detection, or larger mortalities which are really devastating. Therefore, in using laboratory experiments to predict conditions which will cause mortalities in nature, those which kill 25% or 75% of the stocks are of as much interest as those which kill 50%. In the case of the February 6, 1957 tests shown in Fig. 1 they average 0.3°C. respectively below and above the temperatures required to kill 50% of scallops in 48 hours. With few exceptions this is true for all 1956 and 1957 tests. It appears, therefore, that in nature differences in high temperature exposure of as little as 0.3°C. could mean a difference between 25% and 50%, or 50% and 75%, mortality of scallop stocks.

Size Effects

Huntsman and Sparks (1924) noted that in the winter flounder, *Pseudopleuronectes americanus*, susceptibility to high temperature increased with size, although this was not true of other flounder species tested at the same time. Smith (1940) has demonstrated that small starfish tolerate higher temperatures than large, and McLeese (1956) has cited further examples, although he failed to find a relation between size and lethal temperature in the lobsters he used.

Chiasson, Johannes, and the writer have compared lethals for "large" scallops (ranging from 80 to 145 mm. in shell diameter) with those of "small" scallops. Chiasson's small scallops were mostly sexually mature, few being below 77 mm. shell diameter. Johannes's ranged from 40 to 68 mm.; some of the larger were sexually mature but the majority immature. The writer carried out two tests in late 1956 with immature specimens from 47 to 67 mm. and two more in April and August 1957 with immatures between 48 and 78 mm. In no case was there any consistent difference between lethal temperatures for small and large scallops which could be ascribed to their size or state of sexual maturity.

Comparison of Stocks from Different Areas

Johannes conducted several experiments to compare the lethal temperatures of scallops from the Bay of Fundy near Digby, N.S., from the Toney River bed in the southwestern Gulf of St. Lawrence, and from Passamaquoddy Bay, N.B. There was no detectable difference between the Digby and Passamaquoddy Bay stocks. Data from 48-hour lethals comparing Gulf and Passamaquoddy Bay stocks are summarized in Fig. 6.

All tests with Gulf stocks acclimated at about 10 and 15°C. indicate that differences in lethal temperatures between samples collected on July 7 and 23 were no greater than differences between lethal temperatures in successive tests using the July 7 collection alone (Fig. 6). Results from the attempted acclimation at 6.7°C. are similar to those from summer tests with Passamaquoddy Bay stocks

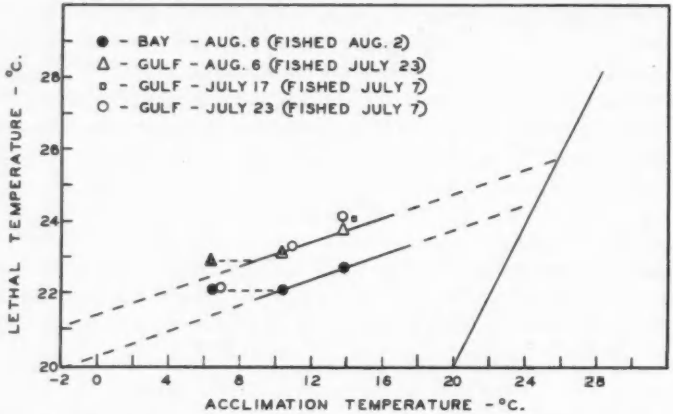

FIG. 6 Comparisons of 48-hour upper lethal temperatures for scallops collected from the southwestern Gulf of St. Lawrence, and from Passamaquoddy Bay in 1956. (Construction line as in Fig. 2.)

described earlier, except that the Gulf scallops collected July 7 were less resistant to high temperature on July 23 than on July 17. The reason for this difference is unknown. Otherwise Gulf stocks show much the same pattern of response to high temperatures as Passamaquoddy stocks, except that their 48-hour upper lethal temperatures were uniformly about 1°C. higher. When 120-hour lethals are used in the comparison, differences in lethals between the 2 stocks are 0.6 or 0.7°C.

There are no records of the water temperatures from which the Gulf scallops were collected which could aid in interpreting this difference. However, we know that the Gulf scallops were fished from a bed off Toney River, N.S., at a depth of 17 fathoms (31 m.). The water in this area is highly stratified in summer, and in July the warm surface layer is usually not thicker than about 5 fathoms (10 m.) (Lauzier, Trites and Hachey, 1957). Bottom temperatures there were likely less than 5°C., whereas the Passamaquoddy scallops were taken from 9°C. The Gulf samples therefore appear to be comparable with Passamaquoddy winter and early spring (5°C.) samples. Fig. 4 shows that these have a 48-hour lethal of about 24°C. after acclimation at 15°C., which corresponds with the lethal temperature for the Gulf stocks acclimated to 15°C.

On the basis of these few observations it seems likely that the difference between Gulf and Passamaquoddy stocks resulted only from a difference in their

temperature experience prior to collection. That is, the data provide no evidence of geographic or racial difference in scallop sensitivity to high temperature, although no adequate search has been made for them.

GENERAL DISCUSSION

Upper lethal temperatures for the giant scallop appear to lie in the low 20's (Centigrade), much the same range found by Brett (1952) for the young of 5 species of Pacific salmon. From standard 48-hour tests using failure of velar response as a criterion of death, the upper lethals for scallops vary from a theoretical minimum of about 19.8°C. for those in summer condition acclimated to the freezing point of sea water, to a maximum of 26.3°C. for those in winter condition acclimated gradually to the highest temperature they can tolerate. Upper incipient lethals, based on 120-hour tests, using weakness as a criterion of death, appear to be uniformly 1°C. below these, or 18.8°C. and 25.3°C. respectively.

Because of seasonal variation in scallop sensitivity to high temperature, rapid acclimation to increased temperature, and remarkably slow loss of high-temperature acclimation when temperatures are decreasing, the incipient upper lethal limits just given have little real meaning in determining the probable effects of high temperature on natural survival. That is, under normal conditions of slow seasonal change in marine climate, scallops will become acclimated to near the highest temperatures they have encountered recently. They will only slowly change this state in reduced temperatures. Therefore, the concept of a scallop in summer condition acclimated to the freezing point of sea water is a fiction. The only upper lethal temperatures which have real meaning under such circumstances are the *minimum seasonal* upper lethals. These are shown for scallops in Fig. 7.

Fig. 7 is derived from the experimental data under the following considerations. Fig. 4 showed the standard 48-hour lethals for scallops collected at different temperatures (equivalent to different seasons) and acclimated to 15°C. But in nature scallops cannot be acclimated to temperatures below those at which collected. Therefore, the point of present interest in Fig. 4 is that where the 15°C. acclimation line intersects an ordinate at the collection temperature of 15°C. This represents the minimum temperature which, in 48 hours, will kill 50% of scallops living at 15°C. The true upper lethal temperature corresponding with this result from the standard 48-hour tests is 1°C. below this (120-hour test, using weakness as a criterion of death) or at 22.3°C. This provides a first point for Fig. 7. A second point is easily derived by drawing a graph like that of Fig. 4, but for animals acclimated to 10°C. Because at any season a drop in acclimation temperature of 5°C. results in a drop of 1°C. in the lethal temperature, this line will be uniformly 1°C. below that of Fig. 4, and the point on it of present interest is where it intersects an ordinate at the collection temperature of 10°C. The acutal minimum seasonal lethal at this point will again be 1°C. below this point derived from the standard 48-hour tests, or at 21.6°C. Other points may be similarly derived, and their locus is shown in Fig. 7.

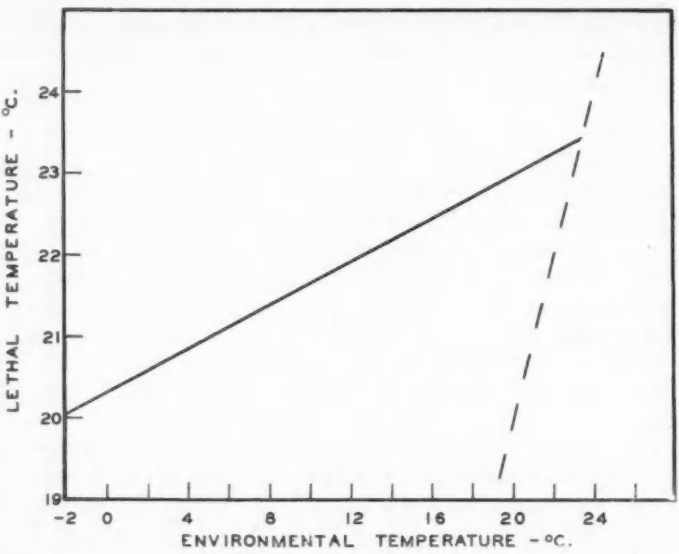

FIG. 7. Upper incipient lethal temperatures for scallops acclimated to normal environmental seasonal temperatures. (Dashed line is a construction line as in Fig. 2.)

The graph in Fig. 7 terminates where it intersects the ordinate at the freezing point of sea water and the diagonal where lethal and environmental temperatures are the same. These points, 20°C. and 23.5°C. respectively, represent the limits of minimum upper lethal temperatures for scallops acclimated to temperature conditions in their natural habitat.

Fig. 7 shows that 50% of a natural scallop population will be killed by exposure for 120 hours (5 days) to a temperature of 23.5°C. or higher. At temperatures below this, the lethal will be lower, depending on past temperature experience. Scallops living at 4°C. have an upper lethal of 20.8°C., while those living at 10°C. have one of 21.6°C. The temperatures required to produce 25% or 75% mortalities will be, as indicated earlier, uniformly 0.3°C. below or above these.

The slope of Fig. 7 indicates that the minimum seasonal lethal temperature rises 1°C. only after a 7.3°C. rise in environmental temperature. This is slower than the response noted earlier to rapid change in acclimation temperature at any one season. The faster rate of adjustment to temperature change therefore takes place only when there is no seasonal "adjustment", and may be used to predict lethal temperature if acclimations above the normal environmental temperature should take place at any particular season, perhaps as a result of unusual hydrographic conditions. Under more normal conditions seasonal adjustments seem likely and Fig. 7 is appropriate.

It appears from the foregoing that in the southwestern Gulf of St. Lawrence, where bottom water temperatures in summer may be only 4 to 8°C., sudden exposure to temperatures of 20.5°C. to 21.1°C. could produce temperature kills. However, it has been pointed out that when scallops are subjected to sudden temperature changes within their "zone of tolerance", they become sluggish in their movements and insensitive to stimuli which normally disturb them. If animals which prey on them are less affected, or adjust more quickly to sudden temperature changes, exposure to marked change in temperature, to "sub-lethal" levels, might be an indirect cause of increased scallop mortality. From data available it appears that any rise in temperature by about 10°C., or any rise to a temperature over 20°C., will expose scallops to the risk of increased depredation for about 24 hours. A drop of only 4 or 5°C. may similarly expose them to depredation for periods of more than a month.

Some writers have suggested that the success and distribution of many species may be limited by the effect of high summer temperature on survival of adults (Hutchins, 1946). In this connection, it is tempting to speculate on the evolutionary significance of our findings. We might have expected that prolonged natural selection for tolerance to high temperature would have produced animals that are more resistant to high temperature in summer, when the selection pressure is greatest, rather than in winter when selection for this characteristic must be negligible. But our observations show that scallops are actually most resistant to high temperature in winter. Similarly Hart (1952) and others (see Brett, 1956) have failed to find geographical variation in temperature resistance in most species of fish examined, and McLeese (1956) found no difference among lobsters from different areas. The same may be true of scallops.

Such findings suggest either that the transmission of genetic characteristics which favour increasing resistance to high temperatures is so complex that distinct genetic strains are unlikely, or that mortalities associated with high temperatures are relatively of less long-term importance to the survival of scallops and a number of other species investigated, than are other features of their environment.

SUMMARY

1. Lethal temperature tests have been performed with scallops, using concepts and methods outlined by Fry (1947).

2. Upper lethal temperatures for scallops are in the low 20's Centigrade, their level depending on previous temperature experience. At any one season the upper lethal temperature is raised 1°C. by a rise of 5°C. in acclimation temperature.

3. The upper lethal temperature is raised moderately rapidly (1.7°C. per day) by acclimation to higher temperature.

4. Loss of the state of acclimation to high temperature is very slow, requiring over 40 days in tanks, and possibly as long as 3 months in nature.

5. Scallop activity is arrested by a sudden rise or fall in temperature. They

quickly adjust to increased temperature, but are extremely slow to recover their normal behaviour when exposed to a sudden decrease in temperature.

6. Reduction in the amount of oxygen in the water in acclimation tanks reduces the lethal temperature.

7. Changes in salinity of test water, of the magnitude likely to occur on scallop beds, do not alter the upper lethal temperature.

8. Upper lethal temperatures are lower for scallops collected from warm water in late summer, than for scallops collected from cold water in late winter.

9. Temperatures lethal to scallops in 48 hours are 0.8°C. higher than those lethal to them in 120 hours.

10. Too severe a criterion of death, such as was used in many of the experiments, results in estimates of 120-hour lethal temperatures which are 0.2 to 0.3°C. higher than the actual.

11. Temperatures required to kill 25% and 75% of a sample of scallops are respectively 0.3°C. below and above those required to kill 50%.

12. There was no apparent effect of size or state of sexual maturity on the upper lethal temperature.

13. Observed differences between the lethal temperatures of scallops collected in the southwestern Gulf of St. Lawrence and Passamaquoddy Bay may be attributed wholly to differences in ambient water temperatures.

14. Minimum seasonal upper lethal temperatures are the only reliable guides for estimating effects of high temperatures on scallop survival in nature. They range from 20°C. for scallops living at the freezing point of sea water, to 23.5°C. for scallops living at the highest summer temperature they can tolerate.

15. Under normal environmental conditions upper lethals will increase by 1°C. only after a 7.3°C. increase in seasonal temperature.

16. Direct temperature death seems likely to occur among scallops in nature after exposure to temperatures between 21°C. to 23.5°C., and in exceptional circumstances after exposure to temperatures between 20 and 21°C.

17. Sudden increases or decreases in temperature to levels which are not directly lethal may arrest normal escape behaviour long enough to increase their exposure to predators. Temperature changes may therefore be indirectly as well as directly responsible for scallop mortalities.

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Shubenacadie Salmon[1]

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ABSTRACT

Salmon from the fishery in the brackish outflow of the Shubenacadie River through its estuary and Cobequid Bay consist mainly of 3-year-old grilse that are much larger than comparable fish taken in Grand Lake at the head of the River, and somewhat larger than comparable fish taken in Minas Channel through which these waters are connected with the Bay of Fundy. These salmon are found to be peculiar also in age composition and thus to form a separate population. That they are large for their age is attributed to exceptionally good estuarial conditions for production of zooplankton and for feeding.

With low rainfall these fish are caught mainly far in the outflow and with high rainfall far out. Their numbers fluctuate greatly for unknown reasons except that utter failure of the grilse in 1951 has been found related to lack of rain when they should have been spawned.

INTRODUCTION

Very gradual shallowing of the Bay of Fundy and of its long extension into Nova Scotia gives great tidal amplitude, even of more than 15 metres where Minas Basin passes into Cobequid Bay, beyond which shallowing stops more and more of the lowering of the water with ebbing tide. The very strong tidal action makes the Bay of Fundy relatively unproductive of life (Huntsman, 1952) and gives a very gradual change from salt water to fresh. Shubenacadie salmon are those taken in the brackish outflow of the Shubenacadie River through its 20-miles long estuary and the 22-miles long Cobequid Bay. They are to be contrasted with those taken outside in the salt water of Minas Channel at the head of the Bay of Fundy, and also with those taken inside in Grand (Shubenacadie) Lake, from which the River arises.

These fish were studied only incidentally during investigation of the lake salmon. The local officers of the Department of Fisheries, Mr. W. A. Fullerton of Shubenacadie and Mr. J. B. Fleury of Truro, provided contacts with fishermen and material from them. Figure 1 is a map of the area involved.

Grand Lake, which is 9 miles long, drains a rocky and lake-studded region of about 150 square miles. It seems to hold its salmon through having a depth of over 30 metres near its mouth. The River below it receives additional drainage from about 1,615 sq. mi. of arable country, mainly through the 35-miles long Stewiacke River to the north. The Shubenacadie and Stewiacke estuaries, in which many of the salmon are caught, are narrow and left by the tide. Cobequid Bay is 5 miles broad and mostly from 2 to 10 metres deep. It receives additional drainage on the south side from about 130 sq. mi., and on the north side from about 715 sq. mi. Minas Basin, between Cobequid Bay and the narrow, deep

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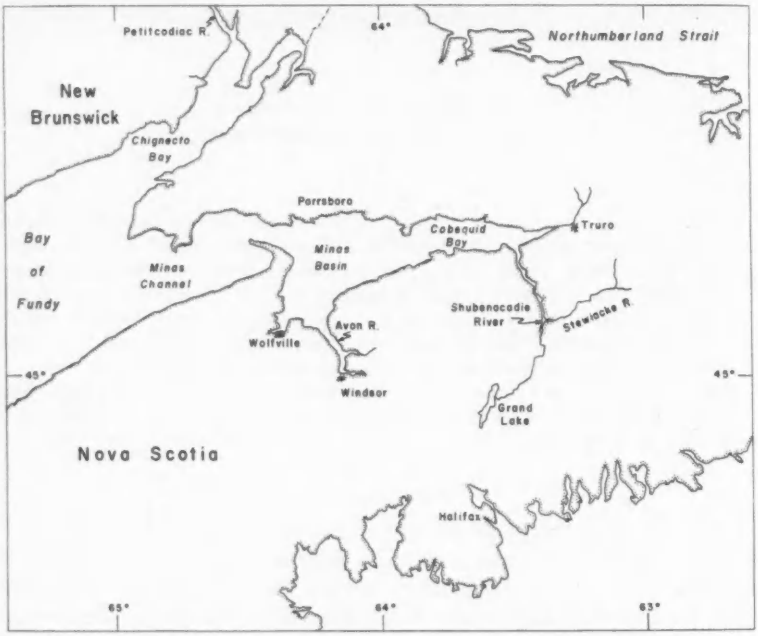

FIG. 1. A map of locations referred to in text.

and tortuous Minas Channel that connects with the Bay of Fundy, is roughly triangular and from 10 to 30 metres deep. Its north side is about 20 miles long. It has a west side about 15 miles long from Minas Channel to its southwest corner, and a southeast side about 25 miles long. It receives additional drainage from 275 sq. mi. on the north and from 1,520 sq. mi. on the south, the latter mainly at the southwest corner, the Avon being the chief river.

The heavy tidal action makes these waters turbulent and turbid and mixes the fresh waters discharged into them with a very large volume of salt water. Consequently there is a voluminous overall circulation or flushing, which is inwards below and outwards above.

THE FISHERY

While the salmon in Grand Lake and the lakes above it are taken by angling, and those in Minas Channel are taken in substantial shore weirs of brush and netting that rise from the bottom near low tide to above high tide, the Shubenacadie salmon are caught in three different ways. Stationary gill nets (set-nets) are erected in the upper part of the estuary. Gill nets (drift-nets) are drifted in the estuary and in the Bay. Traps of brush ("seines"), which are simple weirs, are built around mid-tide level in the outer part of the Bay and in the Basin. These fishing methods are doubtless adapted to local

conditions. Angling is unsuccessful in the sea. Drift netting has been repeatedly tried in the Channel, but without success.

Comparatively few salmon are taken on the south side of Cobequid Bay, which accords with the river discharge being mainly on the north side and with the outflow being turned toward the right by the Coriolis force. During a 10-year period (1898 to 1907) when the fish were most abundant, the catches (Table I) in five districts from the estuary westward along the north side of the Bay and the Basin showed on the average a decrease in this direction, percentages in the successive districts being 47.6, 23.9, 21.3, 4.1 and 2.9. It is a question how comparable the districts are, but their lengths are roughly 20, 9, 9, 9, and 8 miles respectively.

The percentages of the total catch for each year that were taken in the various districts varied from year to year (Table I). River discharge is the chief variable in such an outflow of river water seawards. Discharge records are not available, but monthly records of precipitation are available for three points, Truro at the head of the Bay, Parrsboro on the north side of the Channel and Windsor or Wolfville at the southwest corner of the Basin. The average for these three points for each month (Table II) gives some indication of how the discharge varied. The fish are taken mainly in July and August, but their distribution will depend more or less upon the discharges for some time previous to capture. Also the discharges will depend more or less upon earlier rainfall. The precipitation figures (Table II) for June, July and August of each year have been summed and to each sum has been added half the sum of the figures for the spring months of March, April and May. When the results are put in numerical order from low to high (11.67, 12.83, 12.98, 13.19, 13.38, 13.47, 14.15,

TABLE I. Percentages of Shubenacadie salmon taken in five districts (from Annual Reports of Department of Marine and Fisheries).

Year	1898	1899	1900	1901	1902	1903	1904	1905	1906	1907
Total take (*cwt.*)	441	1045	1140	690	1085	1235	643	628	802	462
Estuary	31.7	22.6	16.8	57.8	48.7	79.0	76.4	36.5	48.0	60.7
Glenholme	29.9	34.3	32.2	13.1	17.0	10.4	14.9	33.5	33.1	20.2
Portapique	27.2	31.0	34.4	24.8	27.1	7.5	8.5	22.4	14.7	15.7
Economy	6.4	9.4	7.0	3.6	6.9	0.6	0.2	2.8	2.5	1.6
Five Is.	4.8	2.7	9.5	9.7	0.3	2.4	0	4.8	1.7	2.1

TABLE II. Average monthly precipitation in inches for Parrsboro, Truro and Wolfville, from *Monthly Records of Meteorological Observations*. (Windsor *vice* Wolfville in 1904, no Truro in 1905 and no Parrsboro in 1907.)

Year	1898	1899	1900	1901	1902	1903	1904	1905	1906	1907
March	3.59	4.75	4.29	2.91	4.69	5.20	3.82	1.01	5.27	2.07
April	5.10	2.14	.485	3.16	1.93	3.55	4.76	.053	4.30	1.72
May	2.55	1.65	3.44	4.33	2.96	0.54	1.48	2.45	5.20	1.79
June	3.30	2.89	3.93	3.30	2.72	1.41	1.70	4.86	3.10	2.36
July	2.35	4.28	2.10	1.02	1.28	3.01	1.79	3.13	3.44	3.61
August	4.83	2.71	3.93	3.46	3.69	2.60	4.31	3.48	1.33	4.44

15.26, 16.10 and 16.25), the percentages of the catch taken in the estuary for the corresponding years are nearly in numerical order from high to low: 79, 76.4, 57.8, 60.7, 48.7, 36.5, 22.6, 48, 31.7 and 16.8. This indicates that the heavier the discharge the smaller the proportion of the fish to be taken in the estuary. It might also be noted that at the other end of the outflow, in the Basin, the lowest percentages of the catch were taken in the six years when there were the highest percentages in the estuary. There is thus evidence that high river discharge shifts the fish outwards and low river discharge shifts them inwards.

THE FISH

Shubenacadie salmon are mainly 3-year-olds that have spent the first two years in the river and a year or somewhat more in the sea, which gives a 4-year period from being spawned to spawning. In 1952, fishermen provided data for 40 salmon from the estuary and 199 from the Bay. Of these only 6 were older than grilse. In the estuary, the grilse averaged 24 inches (21½–26 in.) in total length, and 5.1 lb. in weight (4–7 lb.). In the Bay, they averaged 24.3 in. (21–27 in.) and 5.5 lb. (3½–7¼ lb.). Of 38 fish taken in the Bay in 1953, 30 were grilse averaging 23.3 in. (21–25½ in.) and 5 lb. (3¾–6½ lb.), and 8 were respawners and had been grilse in 1952. These Shubenacadie grilse are larger on the average than those of the same age taken outside in Minas Channel, where grilse were found in data for seven years (1933 to 1936 and 1945 to 1947) to have a mean length of about 21 inches (numbers of individuals of successive lengths from 18 to 24 inches being: 9, 39, 102, 149, 140, 58 and 30). Moreover, the Channel salmon are unspawned fish of various sea ages from post-smolts to fish that have been four, or even more, years in the sea and are very large. The Channel salmon are thus distinct from those inside, which refutes the assumption made (Huntsman, 1931) that they are "related to the rivers emptying into Minas Basin". The Shubenacadie salmon are decidedly different from those in Grand Lake and its tributary waters, which grow much more slowly and are of varied age. Tagging and marking experiments have, however, shown that there is some interchange between these three populations, which are along the course that water takes in going from Lake William near Halifax through these waters to the Bay of Fundy. The Shubenacadie fish are reputedly fatter as well as larger than the others at the same age, but data are lacking as to the condition factor. All this points to exceptionally good feeding conditions for these fish.

FEEDING

Very limited data are yet available for an understanding of these feeding conditions. The Bay of Fundy produces little food because turbidity prevents penetration of light and vertical movements carry the plants down from the surface. Inward transport of zooplankton from the Gulf of Maine fails to take it to the head of the Bay, and Minas Channel is outstandingly barren in food for fish (Jermolajev, 1958). The salmon inside the Channel must depend upon estuarial zooplankton. In the shallow Shubenacadie estuary and Cobequid Bay,

the heavy tides assure a steady supply of water rich in nutrient salts and cannot take the plants far from the surface. Also the fresh water tends to maintain a surface layer for plant growth. There is a brackish water zooplankton (Willey, 1923), which is exceptionally rich (Jermolajev, 1958).

There is a slight tidal bore in the Shubenacadie estuary. The strong bore in the Petitcodiac estuary makes such a heavy suspension of silt as to buoy animals up to the surface, where gulls and other birds can feed upon them. The buoying up of animals in the Shubenacadie estuary does not bring them to the surface, but doubtless brings the fish and their food together, which would enable the salmon to feed well. This requires investigation.

FLUCTUATIONS IN ABUNDANCE

Shubenacadie salmon vary greatly in abundance. The landings for Colchester and Hants Counties, which include the salmon taken on north and south sides respectively of the estuary, the Bay and most of the Basin, show these highs and lows in hundreds of pounds taken in various years: 1903–1,428; 1914–62; 1919–1,100; 1923–54; and 1928–898. In 1951, there was a record low of only 3 hundredweight. It was this virtual disappearance of the fishery that drew our attention to it. The very few fish that we were able to secure late in the season for examination all proved to be respawners. This indicated an utter failure of grilse (usually the bulk of the catch) spawned in 1947 and smolts in 1950. Among the 239 fish examined in 1952 and the 38 fish in 1953, none were found that had been grilse in 1951.

With rainfall the chief variable to change conditions for the salmon, the records pertinent to grilse of 1951 were examined. Spring and summer rainfall showed no unusual character. But rainfall was decidedly peculiar for the autumn of 1947 when they were spawned. These salmon ascend the rivers from tidal water with low temperature and freshets after mid August, and spawn about the end of October. In 1947, there was rather low rainfall in August (average of 1.50 inches), but from September 2 to October 1 an average of 4.69 inches fell, the main falls being on the 2nd and 3rd, 18th and 19th, 22nd and 23rd, and 30th and 1st. After this, for a period of 41 days, very little rain fell, the average for the three points of record being 0.31 inches. Records of the discharges of the Musquodoboit and Rawdon Rivers adjacent to the east show high water early in October, but very low water from October 21 to November 10. There had been nothing comparable in 30 and 35 years of previous records for these rivers. With these conditions, all the salmon could be expected to ascend the rivers early with successive freshets (Huntsman, 1948) and then to be long exposed to very low water. This doubtless prevented spawning, whether through lack of water on the spawning rapids or through poaching can only be surmised. Poaching, which is commonly reported, would be easy for a long time and could have been prevented only at prohibitive cost.

For the Margaree River, a correlation was found between volume of summer flow during the parr stage and abundance of salmon (Huntsman, 1937)

to explain the periodical scarcity of Atlantic salmon revealed by the statistics (Huntsman, 1931). But Shubenacadie salmon did not show the fluctuations in abundance that was general in the Maritimes; rather, they had highest catches when catches generally were in the middle of a long, low period. Nor has it been possible to find any correlation between summer rainfall during the parr stage and their abundance in the fishery for the period (Tables I and II) when they were so abundant as to be well fished and when rainfall data began to be available. There has also been failure to find any effect of the planting of young in the tributary rivers on the fishery catch, for the planting period from 1942 to 1950. Planting of 20,000 underyearlings in 1948, when natural spawning is concluded to have failed to provide any, did not prevent the utter absence of that year-class in the fishery. Plantings dropped from 170,000 fish for the 1941 spawning to 14,400 for 1942 spawning and yet the catch rose from 42 hundredweight in 1945 to 131 in 1946; and with plantings rising from 25,000 to 179,000 for the 1943 and 1944 spawnings, the catch fell from 60 to 16 hundredweight for 1947 and 1948. Nevertheless, the catch rose from 3 to 37 to 57 from 1951 to 1953 when the plantings rose from 20,000 to 135,000 to 317,000 for spawnings of 1947, 1948 and 1949, which could be and was taken to show that planting was effective.

DISCUSSION

The origins of the Shubenacadie salmon are uncertain. Where the smolts from any particular stream go in the sea and where they are to be taken as adults could be, but has not yet been, found out by distinctive marking. Although for the most part the smolts that descend into Grand Lake go no farther seaward, some have been shown by marking to have gone down the Shubenacadie River and through Cobequid Bay and Minas Basin to be taken as post-smolts in Minas Channel. Marking at Moser River of outer Nova Scotia has shown that salmon are caught in the outflows of other rivers than their own. It may, therefore, be expected that the Shubenacadie salmon consist of fish from all of the rivers tributary to these waters.

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Zooplankton of the Inner Bay of Fundy[1]

By E. G. Jermolajev (née Kossiackine)[2]

ABSTRACT

The inner Bay of Fundy and Minas Channel are practically devoid of locally produced zooplankton. The few plankters present are either estuarine species from Minas Basin and Chignecto Bay or immigrants from the Gulf of Maine. The former (*Acartia tonsa, Eurytemora herdmani, Centropages hamatus, Pseudodiaptomus coronatus* and *Canuella canadensis*) are abundant inland with shallowing and heavy river discharge. The latter (*Calanus finmarchicus, Sagitta elegans, Pseudocalanus minutus, Oithona similis* and *Parafavella gigantea*) all show a similar distribution, being abundant in the mouth of the Bay, but declining greatly going inward. Also, *Calanus* specimens from the inner Bay have little or no fat, which indicates a lack of food there.

The extreme paucity of all zooplankton in Minas Channel is apparently caused by heavy and deep turbulence, which prevents development of phytoplankton on which the animals depend for food.

MATERIAL AND PROCEDURE

A marked difference in fish productivity between various parts of the Bay of Fundy has long been known, but evidence to explain the striking contrast between the rich outer and the poor inner parts has been lacking. Although the plankton of the outer Bay has been well studied (Huntsman and Reid, 1921; Gran and Braarud, 1935; Fish, 1936a, b, c; Fish and Johnson, 1937; Huntsman, 1952; and others) data for the inner Bay and its branches to the east (Minas Basin, Cobequid Bay) are almost completely lacking. The limited data now presented seem to have a definite bearing on the low productivity of the inner Bay.

Thanks are due to Dr. A. G. Huntsman for the privilege of working on the material collected in the Bay of Fundy, for his guidance and the advice received in the course of the present investigation.

The material consisted of the following plankton samples:

1. Eighty-six tows made by the motor-boat *E. E. Prince* in August and September of 1920 at various stations (Fig. 1A) in the Bay of Fundy, Minas Channel and Minas Basin. Of these, 14 were vertical tows from bottom to surface with the No. 0 metre net, 29 were horizontal tows at from 18 to 23 metres depth with the No. 0 metre net, and 43 were horizontal tows made with a No. 5 net, either at the surface or at a depth of about 7 metres. Unfortunately, all kinds were not available for all stations.

2. Eleven tows made by the motor-boat *Mallotus* in July, 1951, in Minas Basin, Minas Channel, and along the Nova Scotian cost to Digby Gut. These were horizontal tows with the No. 5 net at a depth of about 7 metres.

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3. Two tows made in Cobequid Bay and one in the Shubenacadie River estuary in July, 1951, with the No. 5 net. The former were made from a motorboat and at some depth not very well controlled, but the tidal turbulence in such shallow water makes this practically unimportant. The tow in the estuary was made with the tidal flow from the bridge at Shubenacadie.

The material has been studied quantitatively by counting the number of individuals of each species in a portion of the sample and calculating therefrom the total number in the tow.

DESCRIPTION OF THE AREA

The Bay of Fundy branches at its head into Chignecto Bay to the north and Minas Basin to the east. The outer Bay has a strong contra-clockwise circulation and heavy tidal action to make the water turbulent and turbid (Gran and Braarud, 1935; Fish and Johnson, 1937; Watson, 1936; Huntsman, 1952). This circulation brings in quite salt water from the Gulf of Maine near the bottom and along the Nova Scotian shore and carries out along the New Brunswick shore water that is of lower salinity and density, largely as a result of discharge from the Saint John River of New Brunswick, midway in the length of the Bay.

The Bay inside the location of this discharge is shallower, the depth decreasing steadily inwards from about 100 metres to begin with. With decrease in depth and increase in tidal amplitude, there results an almost complete absence of vertical stratification of the water (Craigie, 1916; Craigie and Chase, 1918; Watson, 1936), and horizontal circulation is quite slight. The deep water moves slowly and steadily inwards and towards the New Brunswick shore, while the surface water drifts outward and to the Nova Scotian shore. Turbulence and turbidity increase towards the head of the Bay while salinity and density decrease.

From the head of the Bay, the main tidal movement inward is through Minas Channel, whose circulation seems to consist of merely a slow deep inflow and superficial outflow. Salinity and density decrease going inwards. Inside the Channel, in Minas Basin, the circulation seems to be similar to that of the inner Bay, with relatively quiet water in the southern bight which extends south to Windsor. Cobequid Bay, a narrow and shallow continuation of the Basin, has extremely heavy tidal action, with even more than 15 metres amplitude at its mouth.

RESULTS

The plankton is a mixture of true pelagic species, Tintinnoidea, Chaetognatha, Cladocera, Copepoda, and larvae of the benthonic animals. The material also includes typical bottom forms such as harpacticoids, bottom amphipods and Hydracarina, which are not properly planktonic, but merely in suspension, like the silt, which is sometimes very abundant.

On the basis of distribution, Fish and Johnson (1937) divided zooplankters of this region into groups and evaluated the numerical importance of these and of the species. It seems hardly possible to follow this method in handling the present very limited material.

The forms showing the most striking and regular variations in abundance were: *Parafavella gigantea, Sagitta elegans, Calanus finmarchicus, Pseudocalanus minutus, Oithona similis, Acartia tonsa, Eurytemora herdmani, Centropages hamatus* and *Pseudodiaptomus coronatus*. These form two distinct groups, immigrants from the Gulf of Maine, and endemic forms which are purely neritic or estuarine.

Immigrants from the Gulf

Calanus finmarchicus. This is a dominant form in the Gulf of Maine at all seasons of the year (Bigelow, 1926), and is the most important species in the outer Bay of Fundy, always exceeding all the other species in the monthly averages (Fish and Johnson, 1937). The stock of this species enters the Bay from the Gulf in the copepodite stages (Wright, 1926; Fish and Johnson, 1937).

This species occurred (Tables I, II, III, Fig. 1B) in great numbers in the deepest part of the Bay only, from which it was distributed inwards in rapidly decreasing numbers. Only a few moved very far in, and none entered Minas Basin. The quantities recorded were very much greater for the Nova Scotian than for the New Brunswick side of the Bay.

A visual comparison of the amount of oil in the adults collected at 4 stations was made to determine how they varied in condition. In samples of 50 individuals from each of station 187 in the centre of the outer Bay and station 185 a short distance within the inner Bay, the oil to be seen in each individual varied from a large drop occupying the whole length of the thorax from the rostrum back to the end of the fifth segment down to none at all. The numbers of individuals in each of 6 rough grades in amount of oil were as follows:

Station No.	Percentage of thorax occupied by oil				Few small oil drops	None
	100	75	50	25		
187	10	14	17	1	3	5
185	1	2	7	3	8	29

The greatly decreased amount of oil in specimens inside the inner Bay is clearly shown. The very few specimens taken far in the inner Bay show a much poorer condition still. Of 10 specimens at station 183 on the Nova Scotian side, 3 had a few very small drops of oil and the others none at all. Of 10 specimens at station 179 on the New Brunswick side, a female had a drop occupying about 25% of the thorax, another a very small drop, and the others none at all. This indicates lack of food for these copepods in the inner Bay.

Sagitta elegans. This Chaetognath enters the Bay, where the young are more widely distributed than the adults, and does not breed successfully there (Huntsman and Reid, 1921). The 1920 samples showed that adults *Sagitta* are restricted to the deeper parts of the Bay, large specimens (30 to 35 mm. long) being found in large quantities only below 23 metres at station 3. Small *Sagitta* showed a distribution similar to that of *Calanus*, being abundant in the outer

TABLE I. Numbers of the principal zooplankters taken with the No. 0 metre net in the upper 23 metres in the Bay of Fundy and associated waters in 1920.

Station No.	3	169	171	173	174	179	181	181	185	187	190	191	193	194	195	196
Date	Aug. 25	Aug. 25	Aug. 25	Aug. 25	Aug. 26	Sept. 3	Sept. 3	Sept. 10	Sept. 11	Sept. 13	Sept. 4	Sept. 4	Sept. 4	Sept. 8	Sept. 8	Sept. 8
Calanus f.	15975	3709	29700	18125	5440	10	0	0	2037	2850	0	0	0	0	0	0
Sagitta eggs	1	5	1	1	44	2	4	5	7	0	0	0	0	0	0	0
Pseudocalanus m.	0	1	0	1	2	0	0	0	2	0	0	0	0	0	0	0

TABLE II. Numbers of the principal zooplankters taken with the No. 5 net in the upper 7 metres in the Bay of Fundy and associated waters in 1920.

Station No.	3	169	174	176	176	178	179	181	181	183	185	187	190	191	193	194	195	196
Date	Aug. 25	Aug. 25	Aug. 25	Aug. 26	Sept. 11	Aug. 26	Sept. 3	Sept. 3	Sept. 10	Sept. 3	Sept. 11	Sept. 13	Sept. 4	Sept. 4	Sept. 4	Sept. 8	Sept. 8	Sept. 8
Calanus f.	28130	1370	1597	99	2960	4	0	1	0	1	775	10160	0	0	0	0	0	0
Sagitta eggs	1100	575	0	850	2850	1	1	0	0	0	60	1150	0	0	0	0	0	0
Pseudocalanus m.	7900	2125	1375	125	10250	1	0	25	325	400	8570	450	25	0	0	25	0	60
Oithona s.	7700	6025	225	425	7600	75	1	1	150	75	4275	1950	0	0	0	0	0	0
Parafavella g.	2705	150	125	50	4400	0	0	0	0	25	675	2150	0	0	0	0	0	0
Acartia t.	0	0	0	0	0	0	100	0	150	0	0	0	25	0	100	50	450	35760
Eurytemora h.	0	1	0	1	0	0	25	75	475	0	220	0	350	1	500	100	1450	7440
Pseudodiaptomus c.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	3	1200
Centropages h.	500	200	1	1	250	1	900	300	200	25	60	0	225	100	150	100	150	840

TABLE III. Numbers of the principal zooplankters taken with the No. 5 net in the upper 7 metres in the Bay of Fundy and associated waters in 1951.

Station No.	5	8	11	13	14	15	16	17	18	19	20	21	22	23
Date (July)	14	14	14	18	18	19	19	19	19	19	19	10	10	29
Calanus f.	1	0	0	0	0	0	0	2100	12200	0	100	0	0	0
Sagitta eggs	1	0	0	0	0	0	0	0	0	600	600	0	0	0
Pseudocalanus m.	1	0	200	0	200	1	100	23900	39200	44000	200	0	0	0
Oithona s.	0	0	0	0	0	0	0	1100	4100	1	0	0	0	0
Parafavella g.	0	0	0	0	0	0	0	0	100	300	1700	0	0	0
Acartia t.	400	500	600	100	1	100	100	0	0	0	0	29000	25000	0
Eurytemora h.	500	900	2500	200	900	1200	1400	0	0	1	600	500	100	0
Pseudodiaptomus c.	0	0	0	0	0	0	0	0	0	0	0	1500	3200	0
Centropages h.	300	600	700	200	100	1000	1	0	0	0	0	500	4500	0
Canuellea c.	0	0	0	0	0	0	0	0	0	0	0	0	0	136800
Cypria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	116100

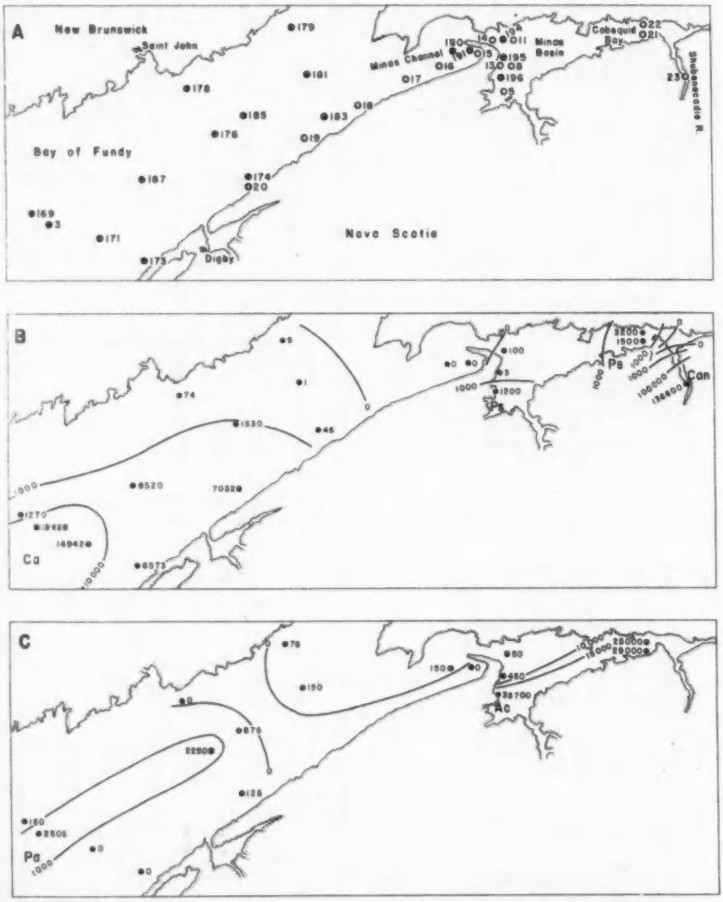

FIG. 1. (A) Plankton stations in Bay of Fundy, Minas Channel, Minas Basin, Cobequid Bay and Shubenacadie River estuary. Solid dots indicate stations worked in 1920, open circles are stations worked in 1951.

(B) Ca: average numbers of *Calanus finmarchicus* in 1920 (No. 0 and No. 5 nets combined; upper 23 m.); Ps: *Pseudodiaptomus coronatus* in 1920 and 1951 (No. 5 net; upper 7 m.); Can: *Canuella canadensis* in 1951 (No. 5 net).

(C) Pa: average numbers of *Parafavella gigantea* in 1920 (No. 5 net; upper 7 m.); Ac: *Acartia tonsa* in 1920 and 1951 (No. 5 net; upper 7 m.).

and scarce in the inner Bay with a much smaller number present on the New Brunswick side. There were none in Minas Channel or in Minas Basin, although in 1951 very small occasional specimens were taken in the Channel.

The floating eggs of *Sagitta* (Tables I–III) were rather numerous in the outer Bay and this distribution suggests that they had been brought in from the Gulf along the Nova Scotian shore. They decrease rapidly in abundance going inwards and disappear in the inner Bay.

Pseudocalanus minutus. This species is second only to *Calanus* as a very important component of the Gulf plankton (Bigelow, 1926), and is also one of the most numerous copepods in the outer Bay (Fish and Johnson, 1937). Being unable to propagate successfully in the Bay (Fish, 1936b), it is an immigrant from the Gulf.

The 1920 and 1951 samples (Tables I–III) show that it becomes much less abundant going into the Bay and towards the New Brunswick shore, which indicates unfavourable conditions. But it is less restricted to the deeper parts of the Bay than *Calanus*. The reason for there being two centres of abundance, one at station 3 in the deep part of the outer Bay and the other in the centre of the Bay just inside the cross-current from Digby to Saint John, is not apparent but they may represent separate indrafts from the Gulf.

Although in both years this species declined in abundance towards the head of the Bay, there were a few in Minas Channel and Minas Basin; it penetrated farther than did *Calanus*.

Oithona similis. (Tables II, III). *Oithona* breeds successfully in the Gulf but not in the Bay (Fish, 1936c), which means it is an immigrant in the Bay. Its distribution is quite similar to that of *Pseudocalanus*, showing the same decrease going inwards and two centres of abundance. It does not, however, go as far inward as the latter, failing to penetrate Minas Channel.

Parafavella gigantea. (Tables II, III; Fig. 1C). This species is evidently an immigrant from the Gulf, decreasing in abundance going inwards. Maximal numbers were found in the outer Bay of Fundy. Apparently it does not reach Minas Channel.

Endemic Species

Acartia tonsa. (Tables II, III; Fig. 1C). This copepod was extremely abundant in the southern bight of Minas Basin in September 1920. A great number of individuals in copepodite stages and an even greater number of mature males and females carrying spermatophores showed that there was active propagation. In July, 1951, it was not very abundant there, but was so in Cobequid Bay, with adults far more numerous than young. It extended out through the Channel in small numbers. In 1920, there were some out in the inner Bay, that conditions were unfavourable for it is indicated by the broken specimens taken at stations 190, 181, 179, 185. There was no indication that any reached the outer Bay.

Eurytemora herdmani. (Tables II, III). This copepod, which is characteristic of the coastal and estuarine or brackish waters of the Gulf (Bigelow, 1926) is

next in importance to the preceding species in Minas Basin. In 1920, it was most abundant in the southern bight and it was found, like that species, out through the Channel into the inner Bay, but not in poor condition. In 1951, it was in fair numbers in the Basin and Channel, but not farther out until station 20 was reached. Its presence there was doubtless due to water from Annapolis Basin; tows made in the latter in 1916 showed fair quantities of it.

Pseudodiaptomus coronatus. (Tables II, III; Fig. 1B). This is a typical brackish-water species, occurring in ponds near Cape Cod (Wilson, 1932) and in the Miramichi estuary (Willey, 1923), but not in the Gulf of Maine (Bigelow, 1926), Bay of Fundy (Fish and Johnson, 1937) or Gulf of St. Lawrence (Willey, 1919). Its abundance in Cobequid Bay and absence in Minas Basin and farther out in July, 1951, show how greatly it is restricted in seaward distribution. But it was in the southern bight of Minas Basin in September, 1920.

Centropages hamatus. (Tables II, III). A centre of abundance in the deepest part of the Bay (station 3) seems to indicate that this species came from the Gulf, since its numbers decrease markedly going inwards. Another centre at the mouth of Chignecto Bay (station 179) indicates dispersal from that area. A third centre in Minas Basin (station 196) shows dispersal from the southern bight outwards into Minas Channel. In 1951, this species was very abundant in Cobequid Bay, with smaller numbers in the southern bight and the Channel.

Careful examination showed that those centred at station 3 in the outer Bay were morphologically distinct from the others. They were big, transparent and slender (♀, 129 to 140 mm.; ♂, 125 to 130 mm.). The others were small (♀, 112 to 114 mm.; ♂, 100 to 110 mm.), of a dark greenish-brown colour and with the back of the genital segment in the female densely covered with short bristles. These were evidently an inland, estuarine form.

Canuella canadensis. This copepod (Fig. 1B) and an unidentified ostracod species of the genus *Cypria* are even more restricted in distribution than any of the above (Table III). They were found only in the Shubenacadie River estuary and, as previously reported by Willey (1923), formed the main bulk of the extremely abundant plankton collected there.

DISCUSSION

The inner Bay and Minas Channel have very little zooplankton and are practically devoid of locally produced forms. The few present come either from the Gulf outside or from Minas Basin and Chignecto Bay inside. It appears that conditions in Minas Channel with an extreme paucity of zooplankton in some way put a stop both to inward extension of immigrants from the Gulf and also to outward extension of endemic estuarine forms.

According to Gran and Braarud (1935), the production of phytoplankton in the Bay of Fundy is very low in spite of the relatively high amount of nutrient salts at all depths. They maintain that, owing to the high turbidity of the water, the light necessary for plant growth penetrates no deeper than 10 metres in Passamaquoddy Bay. Also, vertical transportation of the plants in tidal mixing apparently decreases greatly the length of time the plants

remain sufficiently near the surface to have enough light for growth. This condition, which means little food for the zooplankton, doubtless becomes intensified with heavier tidal action going inwards through the Bay.

The zooplankters which do not reproduce successfully, in the Bay, but are brought in from the Gulf, drop off rapidly in numbers going inwards, indicating that they encounter unfavourable conditions. *Calanus finmarchicus*, the most abundant form, lives elsewhere at more extreme temperatures and salinities than those in the Bay, and therefore other factors must come into play to limit its distribution there.

That turbulence and turbidity prevent the growth of phytoplankton (Gran and Braarud, 1935; Riley, 1946) means that there would be lack of food for the zooplankters. That *Calanus* were found to be gradually losing their fat going into the inner Bay provided evidence that they lacked food. *Calanus* can live on their fat reserves under starvation conditions for about 2 weeks (Fuller and Clarke, 1936). Drift bottles dropped outside the mouth of the Bay reach the New Brunswick shore in 16 or 17 days and Minas Channel in 106 days. With real scarcity of food, *Calanus* would have very little chance of surviing to reach the head of the Bay.

Shelbourne (1957) has shown that an adequate supply of planktonic food is necessary for the survival and development of plaice larvae in the southern North Sea. Where the plankton was poor, the larvae were thin and ill-proportioned. Where it was abundant, they were healthy and robust. The extreme paucity of plankton in the inner Bay as well as the poor condition of the few immigrants there leaves no doubt that fish larvae and larger fish that depend upon plankton for food will be little apt to grow and survive if they remain there.

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The Validity of Otolith Age Determinations for Haddock (*Melanogrammus aeglefinus* L.) from the Lockeport, N.S., Area[1,2]

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ABSTRACT

An analysis of otolith edge types, age compositions, length distributions, and an examination of growth from age–length data as compared to growth from tagging data are presented as evidence for the validity of the otolith method of age determination for Lockeport haddock.

INTRODUCTION

In his study of haddock in Norwegian waters Saetarsdal (1953) has pointed out that haddock scale and otolith data have been used in many investigations without testing the validity of the method for the fish involved. He then demonstrated the validity of methods of aging haddock in Norwegian waters. This paper presents evidence for the validity of the otolith age reading method for haddock found off Lockeport, Nova Scotia. Methods of sampling commercial landings for sizes and ages are described.

SOURCE OF MATERIAL

The inshore Lockeport area (Fig. 1) was selected for study because of continuous quarterly sampling of landings carried out during the years 1946 to 1954. Here, the fishery for haddock is prosecuted almost entirely by hook and line methods. Small longliners (40–45 ft.) and handliners catch most of the fish taken from the inshore grounds from May to October, while medium longliners (45–55 ft.) fish this inshore area during the bad weather months of November to April.

The stocks of haddock exploited in the area are thought to be fairly local. McCracken (1956) tagged haddock in southwestern Nova Scotia waters in 1953. Returns indicated little mixing of haddock from the area with those in other regions.

METHODS

Sampling

Sampling of commercial landings has been carried out as a routine at Lockeport since September of 1946. The data dealt with here include material collected by Mr. D. N. Fitzgerald, from that time until December, 1954. This comprises a series of 53 samples, totalling 11,590 fish.

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[2]Based on part of a thesis accepted by the Faculty of Graduate Studies and Research, McGill University, in partial fulfilment of the requirements for the degree of Master of Science in Zoology.

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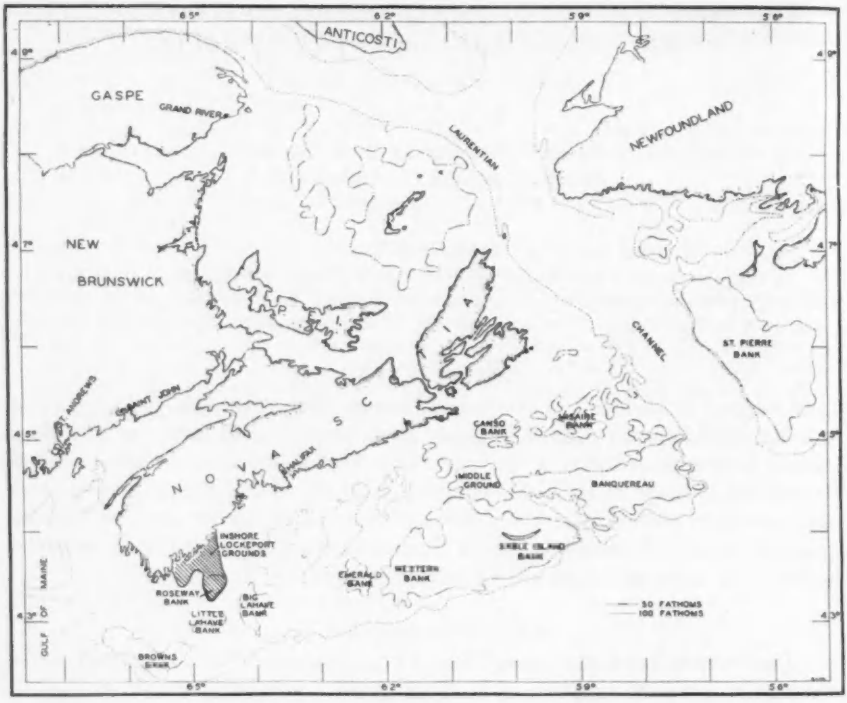

FIG. 1. Principal groundfishing areas off Nova Scotia.

When commercial catches of haddock were landed at Lockeport, the two commercial size categories, scrod (ca. 40–45 cm. in length) and large (over ca. 46 cm.), were sampled separately for length and age. Otoliths were usually taken from one-fifth of the fish measured. In order to weight these sample groups to correspond to amounts of large and scrod landed, weights of each category landed at the fish plant from the area for the sampling day were used. Average weights of individuals in the two categories were obtained by counting the numbers of haddock in boxes of standard weight.

The equation used to obtain the weighting factor for each of the groups was as follows:

$$W_x = \frac{t_x}{T} \times \frac{n}{n_x}$$

where T = total number of fish in catch
t_x = total number of one size category in catch
n = total number of fish sampled
n_x = total number of the size category in the sample

t_x was estimated by taking the average weight of an individual of the size category in question and dividing the total weight of that category landed by this average. T was found as the total $t_x + t_x$ from each size. This procedure for weighting samples of commercial landings of haddock was initiated by Dr. W. R. Martin in 1946.

Examination of Otoliths

Routine examinations of Lockeport haddock otoliths for age determinations have been carried out successively since 1946 by Miss R. I. Peterson, Miss A. R. MacMorran, Mrs. J. M. Stuart and the author. All of these people have had a period of overlap with their successor in order that the interpretation of marks found in the otolith would be consistent.

Until early in 1954 haddock otoliths were kept in vials containing a 50% solution of glycerin with a few crystals of thymol added. However, tests showed that annuli in otoliths from commercial sizes of haddock were just as easily seen after they had been stored dry in envelopes. Since the labour of sampling was reduced by this method, it was adopted.

Otolith age reading was carried out as follows: On the convex side of the sacculus of the otolith there is a longitudinal groove, the sulcus acusticus. The otolith was broken across the interruption in this groove, the fracture surface being perpendicular to the longitudinal axis. An experienced otolith reader could usually make a clean break here by exerting pressure with the thumbs and forefingers. The few poor fractures resulting from this method could be remedied by grinding down the piece that was too long.

The resulting pieces of otolith were imbedded in a cube of modelling clay, the surfaces of the fractures being set flush with the horizontal upper surface of the cube. They were covered with a few drops of 50% glycerin solution. The hyaline and opaque rings found in the cross-section of the otolith were then counted with the aid of a stereoscopic microscope (9×) and reflected blue light. These rings were most easily observed at the pointed end of the cross-section.

Ring counts were translated to ages by a method based on the knowledge of the time of formation of opaque and hyaline zones and the approximate time of the fish's "birthday". For Nova Scotian waters the haddock birthday was arbitrarily established as the first day of February. Although this date may have been about a month early according to data summarized for 1953 spawning, it was convenient for growth studies and ring count translation. February, March and April were then combined as one quarter of the year in which there was little growth in length, and in which hyaline zones were found at the edge of the otoliths of most of these fish.

Table I has been prepared to show the notation used to record readings of otoliths for any month of the year and the standard translation of these readings to age groups. The date of capture was essential to correct translation from zone numbers to ages.

TABLE I. Examples of observed ring counts and edge types on haddock otoliths, and the resulting assignation to age groups.

Time of capture		Number of hyaline zones	Type and width of edge zone	Age group assignation
Quarter of year	Months			
I	Feb.	5	narrow hyaline	5
	Mar.	5	wide hyaline	5
	Apr.	5	narrow opaque	5
		5	wide opaque	5
II	May	5	narrow hyaline	5
	June	5	wide hyaline	5
	July	5	narrow opaque	5
		5	wide opaque	5
III	Aug.	5	narrow hyaline	4[a]
	Sept.	5	wide hyaline	5 (4[a] in Oct.)
	Oct.	5	narrow opaque	5
		5	wide opaque	5
IV	Nov.	5	narrow hyaline	4[a]
	Dec.	5	wide hyaline	4[a]
	Jan.	5	narrow opaque	5
		5	wide opaque	5

[a]In these cases it is assumed that a new hyaline zone has formed at the edge of the otolith before the birthday of the fish in the following February. Therefore, it is not counted as a year-zone for age-group assignation.

VALIDITY OF THE OTOLITH METHOD OF AGE DETERMINATION

SEASONAL CHANGES IN OTOLITH EDGES

The types of marginal deposit found on Lockeport haddock otoliths at different times of the year are shown in Fig. 2. Almost all the otoliths sampled from January to May of each year had hyaline zones at the edges. In the 1954 June sample opaque edges appeared. The peak opaque zone formation at the edge of the otoliths occurred from August to October, and a great predominance of hyaline zones was again observed by December. The failure of any one sample to show 100% opaque zones was usually due to the formation of "false checks" or "subsidiary zones" (Hickling, 1933, p. 30).

The presence of these zones of hyaline material forming within some of the opaque zones necessitated the recording of a hyaline edge even though these would have been recognized and ignored in age reading if the otolith had grown further.

This yearly rhythm of 2 types of zone in otoliths and scales of fish has been discussed by Saetarsdal (1953). The general opinion of the authors he quotes is that seasonal changes of the type recorded in Fig. 2 are good evidence for the validity of the method.

RELATIVE ABUNDANCE OF YEAR-CLASSES

The age compositions of samples of Lockeport haddock landings for the years 1946 to 1954 are shown in Fig. 3. The most abundant single year-class landed by the fishery during this period was the one spawned in 1943. In the

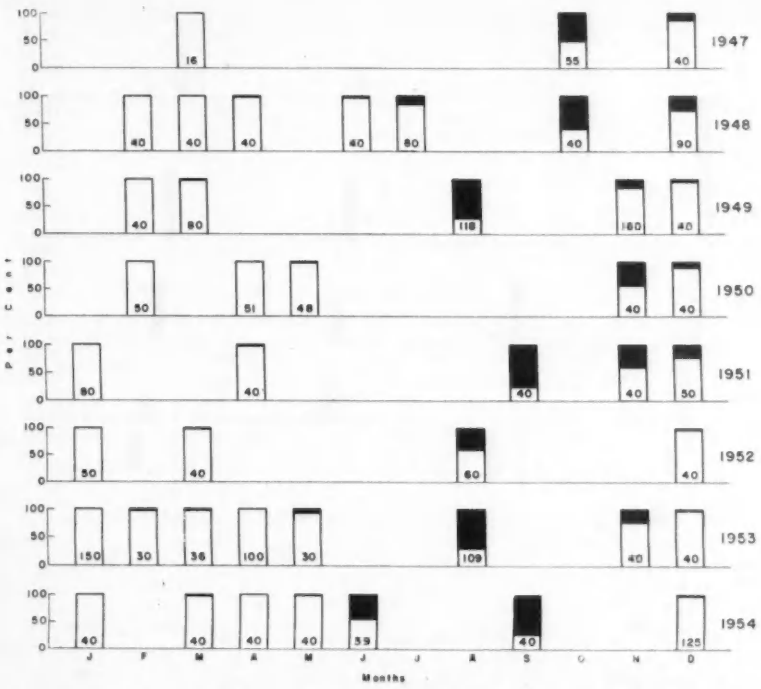

FIG. 2. Type of deposition found in the edge of the cross-section of haddock otoliths from the inshore Lockeport grounds. Black sections indicate the percentage of opaque edges and white sections the percentage of hyaline edges in the otoliths of the sample. The number of fish in each sample is shown.

Figure it is seen to enter the landings in relatively large numbers in the fourth quarter of 1946. The 1943 year-class continued to be dominant in the landings up to the fourth quarter of 1949. Furthermore, it is greater than neighbouring year-classes in the second and fourth quarters of 1950, first quarter of 1951, first quarter of 1953, and first and fourth quarters of 1954. During the same periods a contrast is provided by the relatively small numbers of the 1942 year-class. Continued abundance and scarcity of certain year-classes in continuous sampling of fish populations have been used as evidence of validity of the age determination method by such investigators as Graham (1929), Dannevig (1933), and Hile (1941).

Since the 1943 year-class has passed through the fishery, there has been no single year-class that has been dominant in the landings over a number of years. Four-, five-, six- and seven-year-old fish have made up the bulk of the landings for each quarter, with a number of year-classes contributing. The commercial cull at about 40 cm. fork length eliminates many of the two- and three-year-old haddock from the landings.

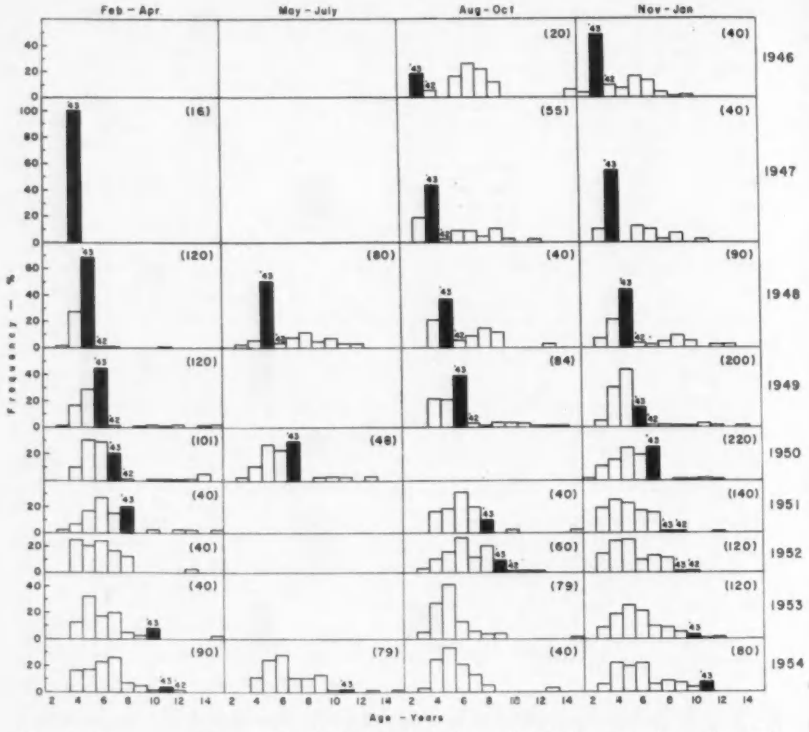

FIG. 3. Age composition of the landed hook-and-line haddock catch from the inshore Lockeport grounds. Numbers of otoliths examined are recorded for each sample. The 1943 year-class is shown in black.

LENGTH DISTRIBUTIONS OF THE 1946–1949 SAMPLES

Graham (1929) and Menon (1950) have shown that if zone formation in scales and otoliths can be correlated with the Petersen method of assigning ages to peaks in length-frequency graphs, the method of aging must produce a majority of correct determinations. Both investigators have indicated that these modes can only be recognized in the first 3 or 4 age groups. Length distributions of older age groups tend to overlap, flattening the curve when the total sample is portrayed.

The Lockeport haddock investigation has indicated that if one extremely abundant year-class appears in the landings, preceded and followed by one or more poor year-classes, the peak produced by the abundant year-class in the length distributions of the samples may be followed for a number of years. In the length distributions of Lockeport haddock landings (Fig. 4) a peak enters the sample distribution in the fourth quarter of 1946. From then until the third quarter of 1949 it is possible to follow this peak through the samples as it moves

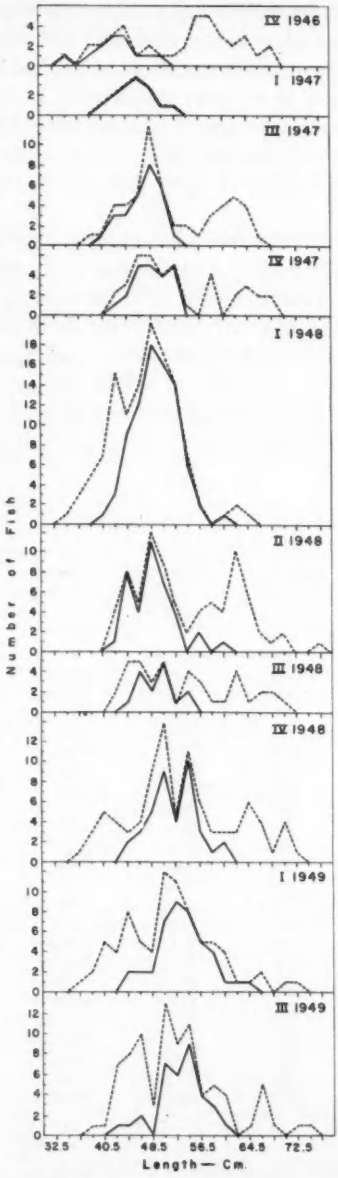

FIG. 4. Length distributions of the haddock landed at Lockeport, N.S., during various quarters of the years 1946 to 1949. Broken lines indicate the length distribution of the total age sample. Solid lines show the length distribution of the 1943 year-class.

along the length scale. Independent age readings for these samples show that the fish sizes in the 1943 year-class correspond with this mode in the overall length composition. In 1946 age determinations showed that the mode was made up of 3-year-old fish, in 1947 they were 4-year-olds, in 1948, 5-year-olds, and in 1949, 6-year-olds. Thus, the evidence demonstrates that this particular group of haddock has added one year mark per year to their otoliths. This is further evidence that the otolith method of aging these fish is valid.

Comparison of Growth from Age–Length and Tagging Data

Lengths of Lockeport haddock at tagging and recapture are available for fish tagged in 1953 (McCracken, 1956). In order to demonstrate that growth data obtained from otolith readings were equivalent to those found for tagged fish, individuals recaptured after approximately one year's freedom were selected. Twenty-three fish met this criterion, of which all but 3 were of ages 5 to 8 (Table II). Comparable growth data from commercial samples of otoliths and lengths are recorded in Table III.

Table II. 1954 recaptures of haddock tagged near Lockeport, N. S., in 1953.

Length at tagging (l_t)	Length at recapture (l_{t+1})	Month of tagging (1953)	Month of recapture (1954)	Age in years at recapture
cm.	*cm.*			
51	53	May	March	6
47	48	May	April	9
52	54	May	April	5
49	50	May	May	6
48	49	May	May	7
53	54	May	May	6
56	58	May	July	...
51	54	May	July	6
47	50	June	May	...
53	56	July	May	7
47	49	July	June	5
58	60	July	June	11
46	51	July	June	6
47	51	July	June	5
64	64	July	August	11
65	66	July	August	...
53	55	July	August	8
48	50	July	August	6
49	52	July	September	6
49	54	July	September	5
47	50	August	May	6
51	56	August	June	6
45	50	August	August	6

In order to plot both age–length and tagging data on the same basis, a straight line transformation was used. This transformation has been employed by Ford (1933) and Walford (1946) for age–length data, and by Manzer and Taylor (1947) and Lindner (1953) for tagging data. Lengths at tagging and age–length means for 1953 (l_t) were plotted against length at recapture and

TABLE III. Ages and mean lengths of haddock sampled at Lockeport in 1953 and 1954.

	Age				
	4	5	6	7	8
1953					
Mean length in cm. (l_t)	46.5	51.9	55.5	58.6	...
Number in sample	21	30	25	12	...
1954					
Mean length in cm. (l_{t+1})	...	49.5	56.0	58.7	59.7
Number in sample	...	26	27	7	10

age–length means for 1954 (l_{t+1}). Least squares fits for the two sets of points gave the following straight line equations (in centimetres):

$$l_{t+1} = 9.8 + 0.86\, l_t \qquad \text{for tagging data}$$

and

$$l_{t+1} = 10.3 + 0.86\, l_t \qquad \text{for age–length data.}$$

These two lines are plotted in Fig. 5, together with the points to which they are fitted.

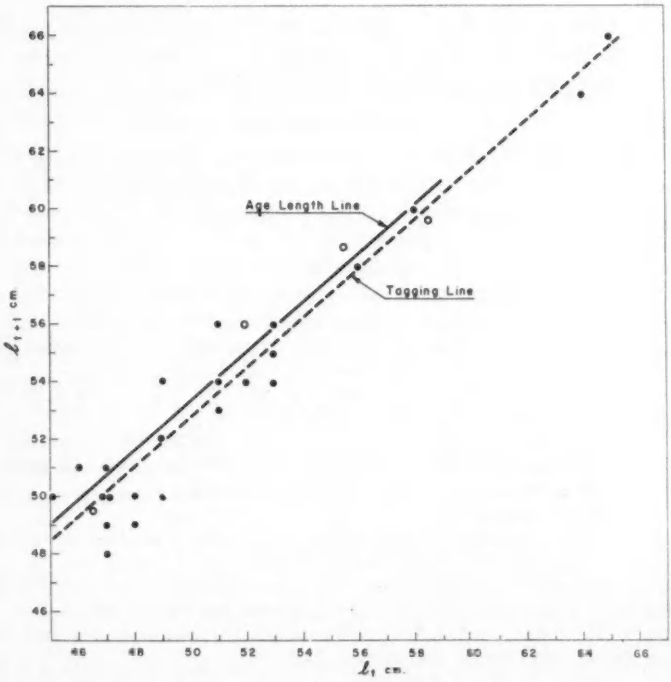

FIG. 5. Straight line transformations for growth in length of Lockeport haddock from tagging and age-length data. Fish lengths (l_t) are plotted against lengths one year later (l_{t+1}). Dots indicate tagging points. Open circles indicate age-length points.

The Figure and the equations show that both lines have the same slope, and they are separated on the l_{t+1} axis by only 0.5 cm. It is evident that the growth parameter arrived at by the otolith age reading method is essentially the same as that calculated by measurements of tagged haddock. This adds a further piece of evidence justifying the use of haddock otoliths as an aging tool.

DISCUSSION

Four types of evidence for the validity of the otolith method of aging Lockeport haddock have been presented in the preceding sections. The data used were taken from samples of commercial landings which consist mainly of fish 3 to 9 years old. Since only 6% of the landings by number are made up of fish over these ages, the otolith method of age determination is considered to be applicable for commercial samples of haddock at Lockeport. Otolith readers have noted in their experience with samples from this and other Nova Scotian areas that annuli are readily distinguished in otoliths from the majority of older haddock, and it is assumed that otolith readings are also valid for haddock over 9 years of age. As noted by Kohler and Clark (1958), this is not true of scale age reading.

Less detailed examinations of data on year-class strengths and otolith edge changes for haddock from other Nova Scotian fishing grounds provide a similar degree of confidence in age readings from their otoliths.

ACKNOWLEDGMENTS

The author wishes to thank Dr. W. R. Martin for guidance during the course of the study, Dr. F. D. McCracken for the use of tagging data, and D. N. Fitzgerald for the efficient sampling of landings at Lockeport.

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Haddock Scale–Otolith Comparisons[1]

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ABSTRACT

Comparisons of scale and otolith age readings have been made for haddock from Subareas 4 and 5 of the ICNAF Convention Area. Percentage of disagreeing readings increases with increasing average age of the fish. In cases of disagreement, scale ages are consistently lower than otolith ages for fish above about 7 years of age in Subarea 5, and for practically all ages in Subarea 4. Variation in results from the 2 methods produces differences in relative strengths of year-classes but has little effect on growth rates.

INTRODUCTION

A preliminary comparison of haddock scale and otolith age readings was carried out by the Fisheries Research Board of Canada's Biological Stations at St. John's and St. Andrews in 1950 (Kohler *et al.*, 1958). Scales from the International Commission for the Northwest Atlantic Fisheries Subareas 3 and 4 fish were read at St. John's while corresponding otoliths were read at St. Andrews. For a total of 576 individuals, 464 (81%) of the corresponding readings agreed. The majority of disagreements were found in readings for old fish, with a tendency toward lower scale than otolith age readings for these individuals.

The present study deals with further comparisons of scale and otolith readings made in 1952, 1953, and 1954 for haddock from Subareas 4 and 5. Scales from these fish were read by United States biologists at Woods Hole and the otoliths were read by St. Andrews personnel. In a total of 764 comparisons, scale and otolith readings agreed in 476 (62%) of the cases. The lower percentage of agreement for this group of readings led to a more detailed analysis of the data arising from them.

METHODS

Sampling

Ten samples were examined for which scales and otoliths were taken from each haddock. Of these samples, 5 were taken by Woods Hole personnel from Subarea 5 fishing grounds and 5 were taken by Canadians from Subarea 4. The map in Fig. 1 shows the distribution of samples on the fishing grounds of Subareas 4 and 5. A list of the samples by number, date, and fishing area can be seen in Table I. The size of the samples varied from 39 to 102 fish.

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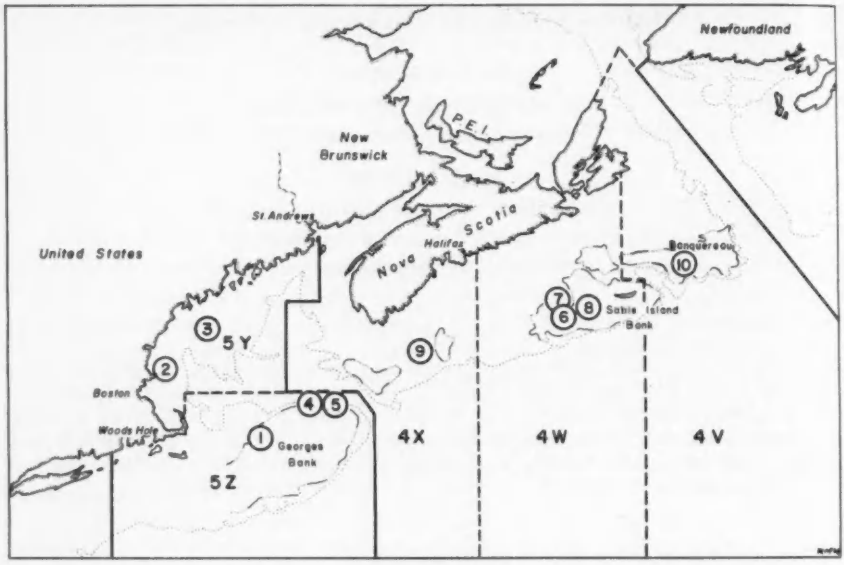


FIG. 1. Map showing locations from which haddock scale-otolith samples were taken. Sample code numbers are in circles. ICNAF subdivisions are outlined.

TABLE I. Results of scale-otolith comparisons for individual samples, 1952–1954.

Sample No.	Month and year taken	Area	ICNAF Subdiv.	Number of fish in sample	Mean age of samples in years			Agreement per sample	
					Scales	Otoliths	Av.	SA 5	SA 4
								%	%
9	Apr./54	Little LaHave	4X	39	6.56	6.72	6.64	...	54
6	Feb./54	Western Bank	4W	60	6.57	6.60	6.58	...	48
8	Apr./54	Sable Island Bank	4W	41	6.02	5.98	6.00	...	51
7	Mar./54	Western Bank	4W	59	5.59	5.97	5.78	...	56
5	Dec./53	Georges Bank	5Z	102	5.65	5.66	5.66	46	...
4	Sept./53	Georges Bank	5Z	99	5.16	5.56	5.36	60	...
3	June/53	Gulf of Maine	5Y	99	5.32	5.26	5.29	66	...
10	Aug./54	Banquereau	4V	65	4.78	5.17	4.98	...	60
2	Apr./53	Gulf of Maine	5Y	100	4.96	4.86	4.91	78	...
1	Dec./52	Georges Bank	5Z	100	2.36	2.35	2.36	90	...

AGE DETERMINATION

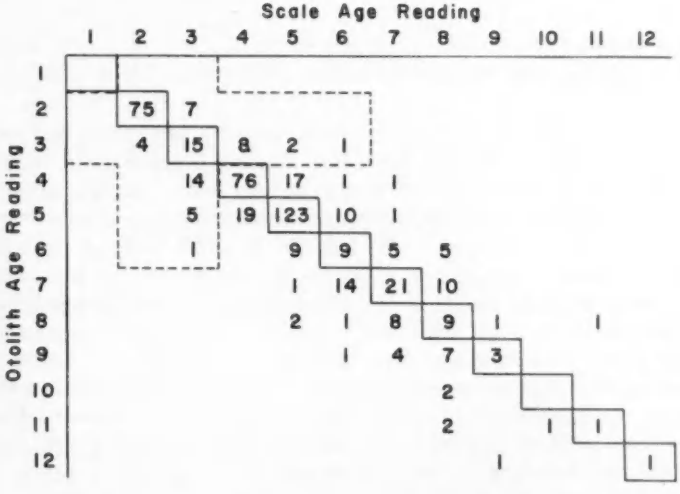
The examination of haddock scales was carried out as follows: As described by Arnold (1951), scale impressions were made on cellulose strips and the impressions were projected at a magnification of 40×. Ages were determined by counting the number of zones of closely spaced, dark circuli which are laid down during winter months. These zones are separated by areas of widely spaced, lighter circuli which are formed in the summer months.

Otoliths were fractured across an interruption in the longitudinal groove, the *sulcus acusticus*, on the convex side. The resulting pieces were imbedded in a cube of modelling clay, the surfaces of the fractures being set flush with the upper surface of the cube. They were covered with a few drops of 50% glycerin solution and examined under reflected blue light through a stereoscopic microscope (9×). Hyaline (winter) zones, separated by opaque (summer) zones, were counted to give the age of the fish.

RESULTS OF COMPARISONS

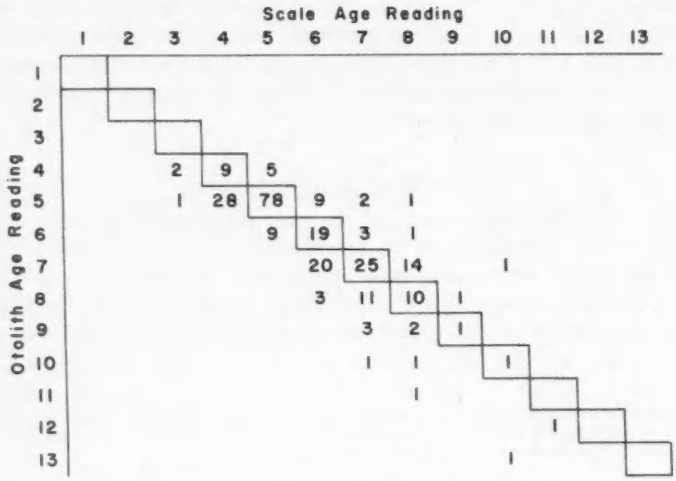
Samples in Table I are arranged in order of descending average age. A comparison of the 5 samples with the higher average ages and those with lower average ages shows better percentage agreement between scale and otolith readings in the latter group. This also holds true within each subarea. Combination of all samples gives 62% agreement for 764 individual scale and otolith readings.

TABLE II. Summary of scale and otolith readings for Sub-area 5 haddock. Dashed lines enclose all fish which were aged 2 or 3 by either method (refer to Table IV). Boxes enclose the numbers of scale and otolith readings in agreement.



In order to show more specific trends in scale–otolith comparisons the data are divided into 2 groups, one containing all Subarea 5 samples and the other containing all Subarea 4 samples. Table II shows the relationship of scale and otolith readings from Subarea 5. In this group of 500 individuals, 67% of the scale and otolith readings agree, 19% of the scale readings are lower than the otolith readings, and 14% of the otolith readings are lower than the scale readings. In Table III data for Subarea 4 fish are plotted in the same way. Here, only

TABLE III. Summary of scale and otolith readings for Sub-area 4 haddock. Boxes enclose the numbers of scale and otolith readings in agreement.



54% of the readings are in agreement; 32% of the scale readings are lower than the otolith readings and 14% of the otolith readings are lower than the scale readings.

Data from the 2 areas have been broken down by age groups and trends in disagreement tested statistically. Ages less than 10 are combined by twos in order to dampen the effect of disagreeing readings from a strong age group on disagreements from an adjacent weak age group. Because of relatively small numbers of old fish, individuals aged 9 to 12 by either method are combined for testing purposes.

The statistical test consists of first summarizing for each group considered the numbers of individuals with scale age lower than otolith age and with otolith age lower than scale age. The resulting numbers are then tested against the hypothesis that they are equal (i.e., that they do not differ significantly from their mean) by calculating chi-square values in the usual manner. When the numbers in either group fall below 5, Yates' correction is applied (cf. Snedecor, pp. 22, 193). As an example, where scale and otolith ages are 2 and 3 (within dotted cross in Table II) calculations were as follows:

	No. of fish
Scale age lower than otolith age	24
Otolith age lower than scale age	18
Mean =	21

$$\chi^2 = \frac{(24-21)^2}{24} + \frac{(18-21)^2}{18} = 0.875.$$

All other groups considered were treated in the same manner. For each chi-square value the probability of obtaining as large or a larger value was looked up in the tables of chi-square (cf. Snedecor, p. 190) interpolating the values to the nearest percentage for small probabilities. The results for Subareas 5 and 4 are tabulated in Tables IV and V, respectively. The differences are interpreted as significant at the 5% level.

Examination of Table IV indicates no statistically significant difference in amounts of the 2 types of disagreement up to about 7 years of age for Subarea 5 haddock. The 8- and 9-year-old group also does not show a difference significant at the level which we have chosen. However, it is evident that in ages over 7 years the otoliths tend to give higher readings than the scales. This is indicated by the chi-square probability figures.

TABLE IV. Comparison of scale and otolith age reading disagreements in Sub-area 5 using the chi-square test.

Scale or otolith age	Number of disagreements	Chi-square value	Probability of a larger chi-square value	Predominant type of disagreement
2 and 3	Sc < Ots 24			
	Ots < Sc 18	$\chi^2 = 0.875$	0.50	No significant difference
3 and 4	Sc < Ots 43			
	Ots < Sc 37	$\chi^2 = 0.453$	0.50	"
4 and 5	Sc < Ots 50			
	Ots < Sc 41	$\chi^2 = 0.899$	0.50	"
5 and 6	Sc < Ots 53			
	Ots < Sc 43	$\chi^2 = 1.053$	0.50	"
6 and 7	Sc < Ots 39			
	Ots < Sc 34	$\chi^2 = 0.344$	0.70	"
7 and 8	Sc < Ots 41			
	Ots < Sc 24	$\chi^2 = 4.773$	0.03	Sc < Ots
8 and 9	Sc < Ots 28			
	Ots < Sc 18	$\chi^2 = 2.282$	0.14	No significant difference
9 to 12	Sc < Ots 18			
	Ots < Sc 3	$\chi^2 = 16.800$	0.01	Sc < Ots

Examination of Table V reveals significant differences in all ages except 8 and 9 for Subarea 4 haddock. In all cases showing differences the scale < otolith group is predominant.

TABLE V. Comparisons of scale and otolith age reading disagreements in Sub-area 4 using the chi-square test.

Scale or otolith age	Number of disagreements	Chi-square value	Probability of a larger chi-square value	Predominant type of disagreement
4 and 5	Sc < Ots 40			
	Ots < Sc 17	$\chi^2 = 11.086$	0.01	Sc < Ots
5 and 6	Sc < Ots 61			
	Ots < Sc 21	$\chi^2 = 25.604$	0.01	Sc < Ots
6 and 7	Sc < Ots 47			
	Ots < Sc 30	$\chi^2 = 3.946$	0.05	Sc < Ots
7 and 8	Sc < Ots 42			
	Ots < Sc 23	$\chi^2 = 6.073$	0.02	Sc < Ots
8 and 9	Sc < Ots 21			
	Ots < Sc 17	$\chi^2 = 0.425$	0.70	No significant difference
9 to 13	Sc < Ots 10			
	Ots < Sc 2	$\chi^2 = 6.189$	0.02	Sc < Ots

EFFECT OF DIFFERING AGE READINGS ON PARAMETERS

The rather extensive disagreement between methods led us to examine its effect on the relative strengths of year-classes and growth.

Age compositions derived from otolith and scale data are plotted in Fig. 2 for Subareas 4 and 5. The populations of fish found in Subarea 5 consist mainly of fish which are 5 years of age or less, and the relative strengths of year-classes agree quite well. Here, overall agreement between methods is 67% and no significant bias in type of disagreement is evident until the fish are about 7 years

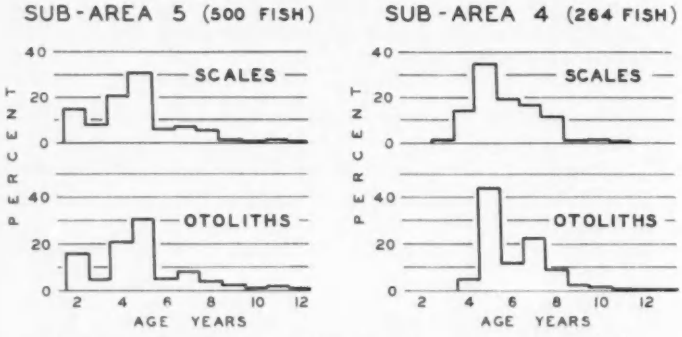


FIG. 2. Haddock age compositions by sub-area and aging method.

old. In Subarea 4 relative strengths of year-classes do not agree well between the two methods. Here, overall agreement is only 54%, and in the majority of cases of disagreement scale readings are lower than otolith readings. One of the effects here is to artificially increase the numbers of 4- and 6-year-olds (the smaller year-classes) and lower the numbers of 5- and 7-year-olds (the larger year-classes) in the scale age composition as compared to the otolith age composition. With consistently lower scale than otolith readings, mortality rates computed from scale ages would be higher than those from otoliths.

Growth data for each sample are plotted in Fig. 3 as average lengths for each age. Where points represent means from 10 or more fish, the average lengths for that age derived from each method lie close together. In 17 out of 19 cases where this occurs, the scale mean length is slightly higher than that found by means of the otolith readings. However, the displacement is usually only a small fraction of a year's increment, and since most of the displacements are in one direction, there is little effect on the estimated growth rates.

Gulland (1955) has published some theoretical considerations of the effects of errors in age readings on various parameters. He has shown that as long as errors do not change greatly from one age to the next, the effect on growth and survival rates is not great. However, such errors will alter the age distribution. Apparently this is what has happened in the tests conducted here.

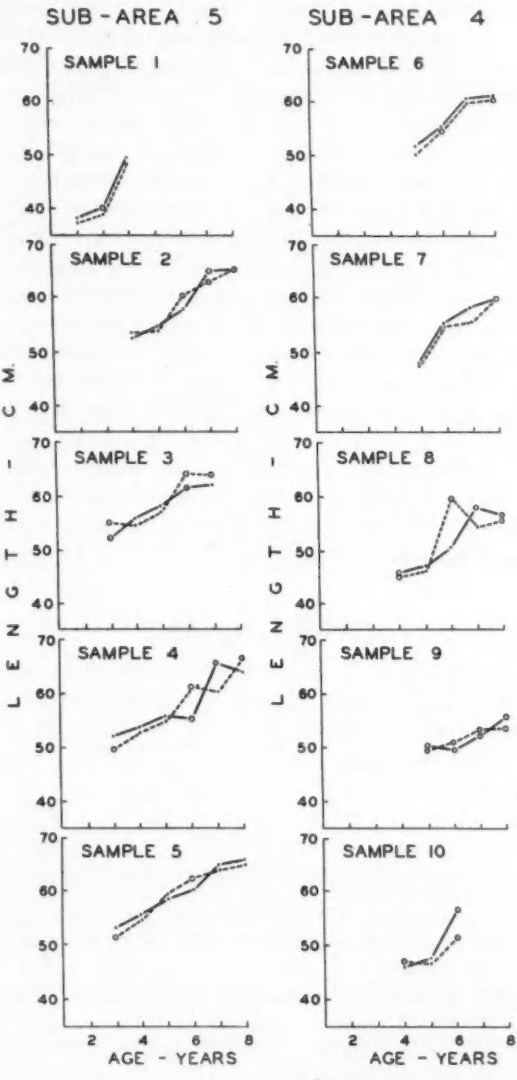


FIG. 3. Haddock growth data by sample and aging method. A solid dot indicates an average from 10 or more fish; an open circle indicates an average for less than 10 fish.

Solid lines: growth from scale readings.

Broken lines: growth from otolith readings.

DISCUSSION

Re-examination and comparison of some of the disagreeing material show that many of the discrepancies are due to differing interpretation of corresponding zones which appear in both the scales and otoliths. Scale readers further point out that the clarity of annuli in the edges of scales diminishes in older fish. A related point to be considered is that the otolith readers were unfamiliar with the annular patterns in material from the relatively young Subarea 5 fish. Scale readers were in the same position regarding interpretation of rings in the scales of older Subarea 4 fish. The greater average age of fish in Subarea 4 tends to provide greater opportunity for conflicting age readings.

Comparison of Tables IV and V indicates that for Subarea 5 haddock there are no statistically significant differences in scale or otolith ages up to an age of about 7 years, from which point scale readings are consistently lower than otolith readings. However, for Subarea 4 where commercial sizes of haddock are older, scale readings are significantly lower than otolith readings at almost all ages sampled. Since re-examinations of disagreeing material showed that otoliths seemed to be a more promising tool for aging old fish than scales, further tests have been carried out to establish the validity of the otolith method. This work will be the subject of another paper. Woods Hole biologists are at present carrying out a further critical review of the scale method, which has been the only one used in Subarea 5. This study will be reported on in the future.

ACKNOWLEDGMENTS

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The Deep Waters in the Laurentian Channel[1]

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ABSTRACT

Data pertinent to the deep warm waters of a three-layer system in the Cabot Strait area of the Laurentian Channel have been collected since 1915. Typical temperature–depth curves indicate that the temperature of the deep layer reaches a maximum at about 250 m. which shows little or no seasonal variations. Observations show warming of the deep layer from the 1920's to the 1950's. This upward trend of temperatures is accompanied by an increase in volume of the deep layer. The deep layer consists of a mixture of "Labrador" and "Slope" waters in which the mixing ratio of the components remains fairly constant from year to year. Fluctuations in temperature of "Labrador" water are reflected by a corresponding change in temperature of the deep layer in the Laurentian Channel. The vertical structure of the waters in the lower Laurentian Channel and the transport of the waters in Cabot Strait suggest that in the deep layers, there is a continuing supply of oceanic waters to the Gulf of St. Lawrence.

INTRODUCTION

The Laurentian Channel is a deep trough that extends from the edge of the Continental Shelf through the Gulf of St. Lawrence and into the estuary of the St. Lawrence (Fig. 1). This channel, which cuts through the Continental Shelf, separates the Grand Banks and the Scotian Shelf. From the edge of the Continental Shelf to Cabot Strait, it has depths ranging approximately from 600 to 400 m. From Cabot Strait inward, for a distance of about 400 miles, it shallows to 200 m. and terminates abruptly in the vicinity of the Saguenay River. Cabot Strait provides the only opening to the deep waters of the Gulf of St. Lawrence. This strait is 56 miles (104 km.) wide and has a maximum depth of 480 m. Its cross section has an area of 35 sq. km. The currents through Cabot Strait have been investigated by Dawson (1913), Sandström (1919), and MacGregor (1956). The circulation in Cabot Strait is featured by an outflowing current along the Cape Breton side and an inflowing current along the Newfoundland side. Dynamic calculations show strongest currents in August and least in April and May.

The waters of the Laurentian Channel are highly stratified (Lauzier and Bailey, 1957). In the summer, a warm surface layer is superimposed on an intermediate cold-water layer overlying a deep warm layer. In winter, a single mixed layer of sub-zero temperature overlies the deep warm layer. A preliminary study of the water mass characteristics by Lauzier and Bailey (1957) showed, by means of T–S relationships, that the deep waters of the Gulf of St. Lawrence, including Cabot Strait, retain their characteristics geographically and seasonally.

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FIG. 1. Bottom topography of the continental shelf and the Gulf of St. Lawrence.

OBSERVATIONS

Oceanographic observations in the Cabot Strait area of the Laurentian Channel have been taken for many years. The first major contribution was made by the Canadian Fisheries Expedition in 1914–15 (Bjerkan, 1919). It was followed by the work of the C.G.S. *Arleux* in 1923 (Huntsman *et al.*, 1954), and the *Cape Agulhas* in 1932–1935 (Thompson and Wilson, 1935, 1936; Wilson and Thompson, 1933, 1934). From 1947 to the present, seasonal observations of oceanographic properties have been taken by the Atlantic Herring Investigation Committee and by the Atlantic Oceanographic Group of the Fisheries Research Board of Canada. The data collected during these expeditions and cruises are pertinent to the area, and have been compiled in order to study the properties of the deep waters of the Laurentian Channel.

TEMPERATURE AND SALINITY VARIATIONS

VERTICAL STRUCTURE

According to the notation used here, the deep layer embraces the waters of salinity higher than 34.0‰ and of temperature generally greater than 4°C. The waters of salinity between 33.0 and 34.0‰, with temperature generally between 1 and 4°C. have been defined as a boundary zone. In the Laurentian Channel, the boundary zone is located just below the cold-water layer.

The temperature and salinity gradients in the boundary zone and the deep layer seem to be independent of the seasons. Figure 2 represents schematically the

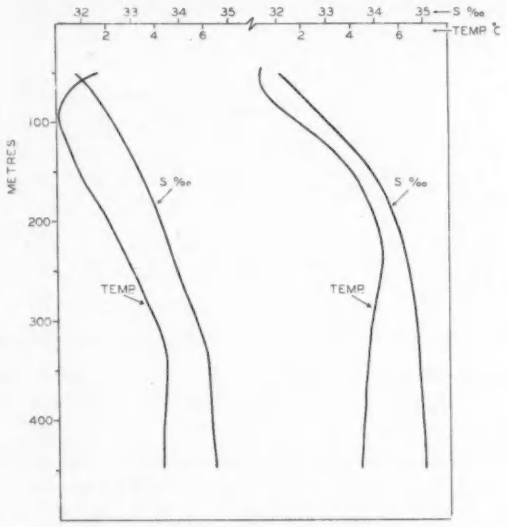

FIG. 2. Schematic vertical distribution of temperature and salinity in Cabot Strait during a cold year (*left*) and a warm year (*right*).

temperature and salinity structure of the waters of the Laurentian Channel in Cabot Strait area for two different types of years. Exclusive of the cold-water layer between 50 and 100 m., the main feature in the two sets of data is the maximum temperature within the deep layer. Irrespective of its depth and of its actual temperature, the water of maximum temperature has approximately the same salinity, 34.6‰. In some years, the maximum temperature within the deep layer is relatively low as compared with other years. In these years, it occurs at greater depths than when the maximum temperature is high. As defined by its salinity, the deep layer varies in its properties, from thin and cool in some years to thick and warm in others. From the data accumulated through the years for the Cabot Strait area, it is possible to show the time variations of such properties.

LONG-TERM VARIATIONS

In Fig. 3, the temperature of two isohalines, 33.0 and 34.0‰, are plotted against time, indicating that a general increase in temperature of these waters has occurred during the last three decades. From the early thirties to the late forties, the warming was more intense for the 34.0‰ water than for 33.0‰ water. In the last 10 years, the 33.0‰ reached a maximum temperature in 1952, while the 34.0‰ reached a maximum a year later.

As mentioned previously, the deep layer of salinity greater than 34.0‰ is featured by a maximum temperature. This section of the water column exhibiting a maximum temperature is called the core of the deep layer. The temperature of the core has been observed to increase considerably over the last three decades

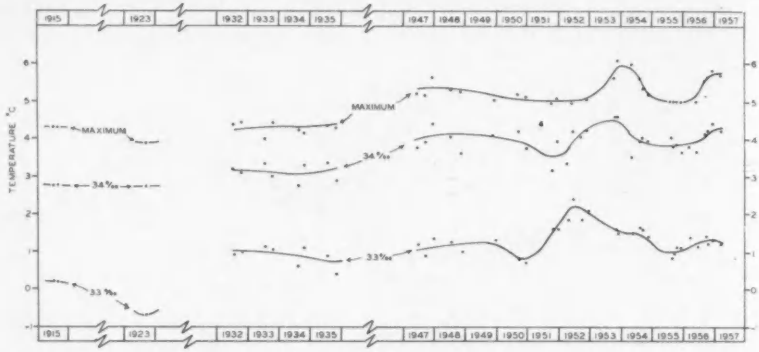

FIG. 3. Temperature variation of isohalines 33.0‰ and 34.0‰ and at the core of the deep layer in Cabot Strait, from 1915 to 1957.

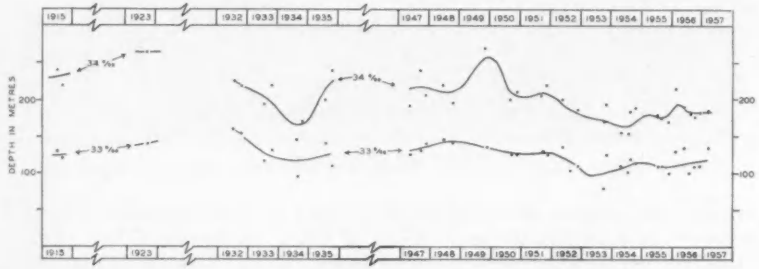

FIG. 4. Depth variation of isohalines 33.0‰ and 34.0‰ in Cabot Strait, from 1915 to 1957.

from about 4.0°C. in the twenties to 6.0°C. in the early fifties (Fig. 3). Also the variability of the temperature of the core from one cruise to the next is much less than the variability of the temperature of the 33.0 and 34.0‰ isohalines. A long-term maximum temperature within the core was reached in 1953–54, somewhat later than at the 34.0‰ level. It is interesting to note that the salinity in the core of the deep layer, which is always greater than 34.0‰, does not show any long-term variations.

In Fig. 4, the variations in depth of the two isohalines, 33.0‰ and 34.0‰, with time, indicate a shallowing of these waters during the last three decades. This shallowing was more pronounced for the 34.0‰ than for the 33.0‰ water. The deep layer showed an increase in volume during the same period the warming occurred.

The variation in the thickness of the boundary zone is related to the variation in volume of the deep layer. This relation is illustrated in Fig. 5. The thickness of the boundary zone is relatively small, when the volume of the deep layer is large, as shown by the depth of the 34.0‰ isohaline.

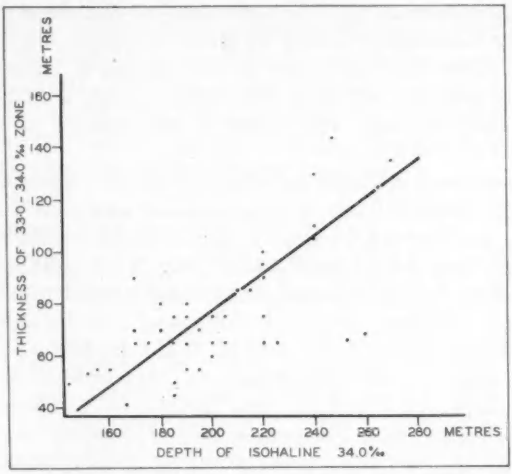

FIG. 5. Relationship between the thickness of the boundary zone and the depth of isohaline 34.0‰ in Cabot Strait.

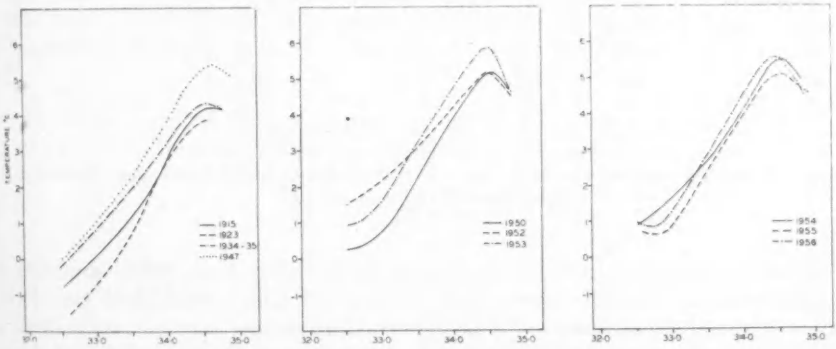

FIG. 6. Average T–S relationships of the deep waters in Cabot Strait at various times from 1915 to 1956.

WATER MASS CHARACTERISTICS

The temperature–salinity (T–S) relationships for the waters of the Laurentian Channel in Cabot Strait have always shown the same general pattern. Only part of the data is illustrated in Fig. 6 to give representative T–S curves from 1915 to 1956. Each curve represents the average T–S relationship of all the data collected during the crossing of the strait within the period mentioned. The T–S relationships are given only for the waters underneath the cold-water layer, where the seasonal variations are negligible. The three sets of T–S diagrams show that the maximum temperature occurs at an average salinity of 34.6‰.

The consistent pattern of the T–S curves suggests that these deep waters are formed outside the Laurentian Channel. To follow McLellan's suggestion (1957a), the deep coastal waters may be formed by the mixture of Labrador water and Slope water. More recently, McLellan (MS, 1957b) made a distinction between the waters in Cabot Strait and the waters at the entrance to the Laurentian Channel.

Few data have been collected in either the lower Laurentian Channel or the entrance to the channel. Some of these data are shown on T–S diagrams to exhibit the differences between the three groups of curves: at the entrance to the channel (Fig. 7, a), lower Laurentian Channel (Fig. 7, b), and Cabot Strait (Fig. 7, c). The variability of the properties of the water mass at the entrance to the

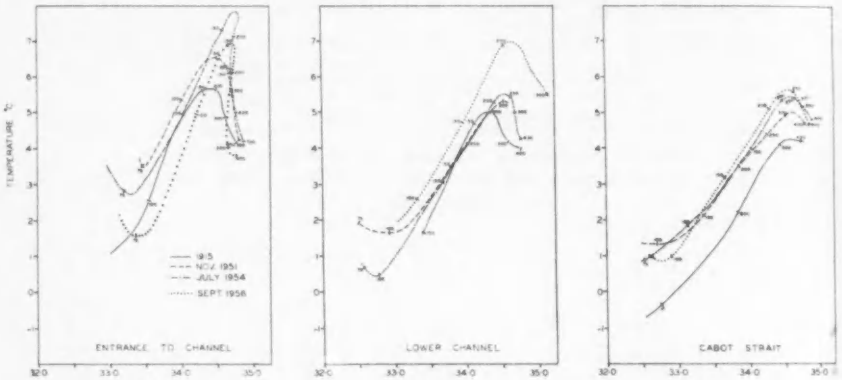

FIG. 7. T–S relationships of the deep waters from the entrance to the Laurentian Channel to Cabot Strait during four cruises.

channel contrasts with that of the water mass in Cabit Strait. Such variability suggests that the coastal waters found between the Continental Shelf and the Slope Water at the entrance to the Laurentian Channel represent an intermediate step in the formation of the deep waters of the channel. Further mixing of the deep coastal waters with water of Labrador Current origin therefore takes place in the lower Laurentian Channel south of Cabot Strait. A small branch of Labrador water penetrates the deep channel between Newfoundland and the Grand Banks and eventually reaches the Laurentian Channel north of St. Pierre Bank.

MIXING RATIOS

As pointed out by McLellan (1957a) the deep coastal waters, because of their geographical position, are possibly formed by the mixture of Labrador and Slope waters. He assumed that the waters in the Laurentian Channel have more persistent characteristics than the waters off the Continental Shelf and that they

would be formed by the mixture of Labrador and Slope waters with proportions of Labrador waters varying from 67% to 38%. At the time, the data of only one cruise were considered. Data from a large number of cruises from 1915 to 1956 are now being considered. The T–S curves (Fig. 6) show some common characteristics such as a maximum temperature at approximately 34.6‰. This point has been defined earlier as the core of the deep layer.

(A) THE CORE OF THE DEEP LAYER

The temperature in the core of the deep layer varied through the years (Fig. 3). The T–S relationships depicting warm, average and cold waters in the core of the deep layer have been used to study the possible mixture of Labrador and Slope waters as components of the core. The T–S relationships of Slope water are taken from McLellan (1957a), and those of the Labrador water from the data of the International Ice Patrol. Three possible T–S relationships of Labrador waters were used, representing cold, average, and warm waters in the Newfoundland area. It is assumed that the mixing takes place along straight lines on a T–S diagram between waters of equal density (same initial σ_t). It was found that the core of the deep layer may be formed by a mixture of the two bodies of water in approximately the same proportions. The results, shown in Table I, indicate that if the mixture of Slope and Labrador waters takes place in the same proportion from year to year, the temperature of the core of the deep layer in the Laurentian Channel is related to the temperature of the Labrador water.

TABLE I. The constitution of the core of the deep layer of the Laurentian Channel from Slope water and Labrador water.

Period	Initial σ_t	σ_t at maximum temperature	Proportion of Labrador water
			%
Cold	27.33	27.40	49
Average	27.22	27.32	47
Warm	27.10	23.23	44

(B) THE DEEP LAYER IN CABOT STRAIT

The possible mixing of Labrador and Slope waters, at the same initial σ_t, was next considered to produce the deep layer as a whole in the Laurentian Channel, under average and extreme temperature conditions. The results are shown in Table II. The proportions of Labrador water involved varied by nearly 30% from lighter to heavier waters. Labrador water predominated in the first case and the Slope water in the second. At all σ_t levels, the proportions of Labrador waters involved in this type of mixing were greater for the production of cold deep waters than for the production of warm deep waters in Cabot Strait. The results obtained by McLellan (1957a), given in Table II, show that he had considered the mixing at the time the temperature conditions were average.

(c) THE DEEP LAYER IN THE LOWER LAURENTIAN CHANNEL AND AT THE ENTRANCE

As shown in Fig. 7, the T–S relationships vary greatly from the entrance to the Laurentian Channel to Cabot Strait. For the four cases considered, it was found that with the waters of salinity greater than 34.0‰, the proportions of Labrador water generally increase from the entrance to the channel to Cabot Strait, with most of the increase occurring near the entrance. However, at the

TABLE II. The constitution of the deep waters of the Laurentian Channel from Slope water and Labrador water.

Initial σ_t	Proportion of Labrador water			
	Temperature conditions			After McLellan
	Warm	Average	Cold	
	%	%	%	%
26.70	66	75	76	...
26.80	60	67	69	67
26.90	55	63	66	63
27.00	48	58	63	59
27.10	44	52	58	53
27.20	41	47	56	48
27.30	38	42	51	43
27.40	35	40	49	39
27.50	31	38	48	38

entrance outside the Continental Shelf, the variations of the proportions of Labrador water are erratic as compared with those in Cabot Strait. Such conditions can be seen from the T–S relationships. These conditions are considered to be the initial steps of mixing which Eckart (1948) defines as stirring.

(d) OTHER TYPES OF MIXING

So far we have considered the mixing at the same initial σ_t, and it has been shown that in order to form the deep waters of the Laurentian Channel, the two bodies of water, Labrador and Slope, would have to mix in variable proportions depending on the initial density. It may be assumed that the mixing of two bodies of water occurs between components at the same depth or between components at different depths but the depth difference is constant in the water column. It was found that if Labrador water at depth z is mixed with Slope water of depth $z + 50$ m., in proportions varying from 60 to 70% of Labrador water, the resultant mixture will have T–S relationships very similar to those of the deep waters of the Laurentian Channel. Such mixing has been studied for three types of deep waters in Cabot Strait, cold, average, and warm, as it was done for possible mixing at the same initial σ_t. The results are given in Table III. Evidence pointing towards the constancy of mixing ratios or proportions of Labrador water is even more pronounced by making the assumption that mixing in both components takes place at different σ_t rather than at the same initial σ_t.

TABLE III. The constitution of the deep waters of the Laurentian Channel from Slope water and Labrador water, mixing at depths $z + 50$.

σ_t Deep waters of Laurentian Channel	Proportions of Labrador water under temperature conditions:		
	Warm	Average	Cold
	%	%	%
27.10	63	...	...
27.20	60	67	70
27.30	64	66	70
27.40	66	64	70
27.50	64	60	69

AVERAGE DENSITY DISTRIBUTION IN THE LOWER LAURENTIAN CHANNEL

From the entrance to the Lower Laurentian Channel to Cabot Strait, the average vertical structure of the water mass changes in such a way that the isopycnals are sloping down towards Cabot Strait. For instance, waters of σ_t value of 26.8 and 27.4 were respectively at 90 and 230 m. at the entrance to the

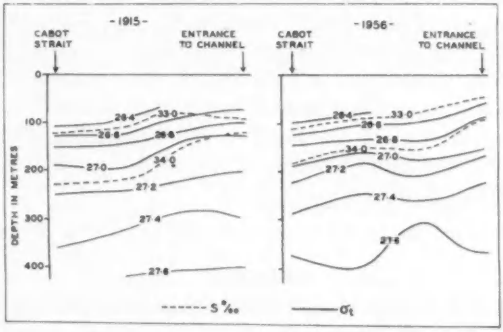

FIG. 8. Vertical density and salinity distribution in the lower Laurentian Channel from Cabot Strait to the entrance of the Channel in 1915 and in 1956.

channel, and at 140 and 290 m. respectively in Cabot Strait. Referring back to the deep layer in Cabot Strait, the waters of salinity greater than 34.0‰ form a wedge in the channel. The 34.0‰ isohaline tilts downward reaching a maximum depth in Cabot Strait. The two cases shown in Fig. 8 illustrate conditions described previously for Cabot Strait only. In 1915, the conditions are those of a cold year, with a deep 34.0‰ isohaline, a relatively small volume of the deep layer, and a thick boundary zone, 33.0–34.0‰ in most of the channel. In 1956, the conditions are those of a relatively warm year, with a shallower 34.0‰ isohaline, a relatively large volume of the deep layer, and a thinner boundary

zone. It seems then that such fluctuations occurring from cold to warm years are not only characteristic to Cabot Strait but also to most of the lower Laurentian Channel.

Movement of the Deep Layer

The scarcity of data makes it difficult to draw precise conclusions regarding the movement of the deep layer in the Laurentian Channel. However, the volume transport data in Cabot Strait as compiled by MacGregor (1956) can be used to approximate the average conditions of flow of the deep waters in the Laurentian Channel. Assuming that the net transport through Cabot Strait is zero, it has been estimated that the deep water layer is generally flowing into the Gulf of St. Lawrence. In one case, the flow of deep water was in a southeasterly direction or out of the gulf. The net transport of the deep waters in Cabot Strait varied from 60 to 430 thousand cu.m./sec. which represents between 10 and 40% of the total inflowing waters through Cabot Strait. The direction of flow of water within the boundary zone is not always the same as that of the deep-water layer.

The wedge-like structure of the deep-water layer in the lower Laurentian Channel and the general direction of flow of such a layer in Cabot Strait, suggest that the deep waters are supplied almost constantly to the Gulf of St. Lawrence. This is the only supply of high-salinity water to the gulf. High-salinity waters are found all along the Laurentian Channel. They retain the same T–S relationships as those of the deep water layer in Cabot Strait. The gradual shallowing of the bottom cuts off in the upper Laurentian Channel some of the higher-salinity water observed in Cabot Strait. At the head of the Laurentian Channel, near the Saguenay River, the remaining portion of the deep layer is used for mixing in the production of part of the Gaspe Current.

SUMMARY

1. Properties of the deep waters of the Laurentian Channel in Cabot Strait area have been studied. The deep-water layer, of salinity greater than 34.0‰, is part of a three-layer system. It is characterized by a maximum temperature at a salinity of 34.6‰.

2. Long-term variations in the temperature and volume of the deep layer have been observed, particularly warming of the deep waters from about 4.0°C. to 6.0°C. in the last three decades. This layer showed an increase in volume at about the same time the warming occurred.

3. T–S relationships of the deep waters of the Laurentian Channel have been used to study the formation of this layer by a mixture of Labrador water and Slope water. Fluctuations in temperature of Labrador water are reflected by a corresponding change in temperature of the deep layer in the channel. A persistent feature is the constancy of proportion of Labrador water in the core of the deep layer.

4. The properties of the deep waters at the entrance to the Laurentian Channel have been compared to those of the waters of the Cabot Strait area.

It is suggested that the coastal waters at the entrance to the channel represent an intermediate step in the formation of the deep waters of the channel, and that further mixing occurs in the lower channel, south of Cabot Strait.

5. The vertical structure of the deep-water layer in the lower Laurentian Channel and the general direction of flow of such a layer in Cabot Strait, suggest that the deep waters are supplied almost constantly to the Gulf of St. Lawrence.

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Fatness of Small Herring in the Bay of Fundy[1]

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ABSTRACT

Fat determinations, by ether extraction, were made on 205 samples of "sardine" herring (*Clupea harengus* L.) from the Quoddy region of the Bay of Fundy on the east coast of Canada. The period covered was from 1942 to 1952. The fat content was lowest in April to June and highest from August to November, with few exceptions. It varied between 1.2% and 27.5% of the wet weight of the fish. There was marked variation from year to year. Until sexual maturity was reached, the fatness increased with size. The herring were extremely fat in the winter of 1942–43 and quite poor in the next winter; a remote connection with plankton abundance is discussed. Certain regions are noted for very high fatness. A fungus disease did not greatly affect the fatness of recovering fish.

INTRODUCTION

Small herring (*Clupea harengus* L.), known locally as "sardines", are caught in large quantities along the New Brunswick shore of the Bay of Fundy and along the coast of Maine. Despite their commercial importance few reports of their chemical make-up have been published. Battle *et al.* (1936) estimated their relative fatness by determining the condition factor. Leim (1943) published preliminary results based on actual fat determinations. Studies on the fat content of larger herring have been reported by various workers (Leim, 1957).

METHOD

Small herring were selected from commercial weir and purse seine catches from 1942 to 1952, using only unsalted fish. From 30 to 80 fish were chosen. They were then rapidly frozen and, on the following day, run through a chilled meat chopper. The resultant material was thoroughly mixed while in a freezer room. Samples were taken to the laboratory, weighed, and mixed with anhydrous sodium sulphate and extracted with ether in a Soxhlet apparatus. The weight of the dried ether extract has been expressed as a percentage of the wet weight of the fish. It consisted of fat and related substances which are ether-soluble.

Some differences in procedure developed as the investigation went on. From 1942 to 1946 inclusive, heads and tails were removed from the fish before freezing; thus these results apply to the portion of the fish that is normally canned. From 1947 on, whole fish were used, since the purpose was to compare small herring with large, and fish meal was being thought of as the chief use for the latter (Leim, 1957).

As the investigation proceeded it was realized that, within a sample, larger fish were fatter than smaller ones. Battle *et al.* (1936) had indicated such a trend. From mid-1943 on, samples were divided on the basis of size. The vagaries of

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size-distribution of the catches prevented the rigorous size choice that would have been desirable.

Determinations of fat content by the Soxhlet method were in duplicate. Many additional determinations were made using the modified Gerber method as described by Johnston (1942). The results were not reliable; this matter was discussed briefly by Leim (1957).

THE MATERIAL

Most of the small herring analyzed were caught in weirs and purse seines operated in the Quoddy region of the lower Bay of Fundy; occasionally samples were available from Saint John Harbour and Grand Manan Island.

The numbers of primary samples were: 21 in 1942, 41 in 1943, 38 in 1944, 27 in 1945, 11 in 1946, 14 in 1947, 15 in 1948, 13 in 1949, 17 in 1950, 3 in 1951, and 5 in 1952. As these 205 samples were usually divided into two or more size groups and were run in duplicate the total number of ether extract determinations was in the neighbourhood of 900.

THE RESULTS

The data are voluminous and detailed tables of all figures are available in a manuscript report which is deposited at the Biological Station, St. Andrews, N.B. Only parts that are significant for the discussion are included here.

In general, the highest fat value found was 27.5% (Harbour du Loutre, N.B., October 19, 1945); the lowest value found was 1.2% (Saint John Harbour, N.B., May 17, 1950).

(a) Variation of Fatness with Size

Early in the investigation it was found that the larger fish were fatter than the smaller ones in practically every sample. This rule almost always held with fish under 23 cm. total length. Occasionally sexually maturing fish were encountered in size ranges above 28 centimetres total length. They showed a marked reduction in fat content. A typical example is given in Table I.

Table I. Fat content of herring, Chatty's Point, N.B., September 11, 1944.

Greatest total length	Fish in sample	Sex	Fat content
cm.	*no.*		%
10.0—11.5	40	?	8.0
14.0—15.0	16	?	9.7
18.0—19.0	6	?	16.7
28.0—31.5	2	M	7.2

The same order, with less spreading, is shown in winter and spring samples. Examples are given in Table II.

TABLE II. Fat content of small and medium herring in winter and spring.

Place	Date	Greatest total length	Fish in sample	Fat content
		cm.	*no.*	%
Beaver Harbour	February 26/45	9.0	23	2.5
"	"	10.0—10.5	48	3.5
"	"	12.0—12.5	45	3.4
"	"	14.5	2	5.0[a]
Pocologan	March 7/47	13.0—13.5	42	7.3
"	"	16.5—17.0	12	10.6
"	April 11/47	12.5—13.0	31	6.4
"	"	16.5—17.0	22	10.0
"	"	19.5—22.0	8	6.0[b]

[a]Approximate. Calculated from Gerber value.
[b]One of the occasional exceptions to the rule that larger fish are fatter.

(b) VARIATION OF FATNESS WITH SEASON AND YEAR

It was found that the fat content of the small herring varied seasonally and also from year to year. The fish were poorest in the months of April to June inclusive in most years. The highest fat contents usually occurred from August to November, but in 1943 January and February were highest. This is associated with the surprisingly fat condition of the fish in the winter of 1942–43, a circumstance that will be referred to later. As the samples were not segregated as to size until Septmber 1943, the best comparison cannot be made until after that. Results up to August 1943 are summarized in Table III.

TABLE III. Fat content of small herring, March 1942 to August 1943.

Month	Number of samples	Highest fat content	Lowest fat content	Average fat content
1942		%	%	%
March	1	...	...	13.7
April	2	10.5	9.1	9.8
June	4	12.7	5.2	8.1
July	6	9.1	3.6	6.5
August	5	14.4	8.4	10.9
September	2	16.1	9.8	12.9
October	2	13.4	9.3	11.3
December	1	...	...	15.5
1943				
January	1	...	...	20.3
February	4	20.1	16.9	18.4
March	2	16.0	13.4	14.7
April	3	13.9	7.1	11.2
May	7	8.0	3.0	6.1
June	6	13.5	6.7	8.4
July	6	19.0	6.1	11.4
August	2	13.3	5.4	8.5

After September 1943 the sizes were segregated; the results for two size groups are shown in Table IV.

TABLE IV. Fat content of small herring, September 1943 to July 1952.

Month and year	Number of samples	Highest fat content	Lowest fat content	Average fat content	
				7.0–14.0 cm.	14.5 cm. and up
		%	%	%	%
1943					
September	4	20.4	8.3	11.6	15.7
October	2	8.7	7.3	8.0	...
November	3	9.8	6.5	7.2	9.4
December	1	6.0	6.0	6.0	...
1944					
January	4	12.5	4.6	7.4	9.6
February	1	4.1	4.5	4.5	5.1
March	1	3.5	4.2	3.5	4.2
April	2	1.6	2.0	1.8	1.7
May	2	6.9	2.5	2.5	5.1
June	5	13.9	4.2	6.9	9.6
July	9	17.3	3.8	8.2	13.8
August	4	14.6	2.9	4.4	9.8
September	3	12.7	6.8	7.6	12.0
October	4	13.1	6.4	8.5	11.6
November	2	11.4	5.3	5.3	9.8
1945					
January	1	7.0	5.7	5.7	7.0
February	1	3.2	3.2	3.2	...
March	3	4.1	3.4	3.7	...
April	3	3.7	2.5	2.8	3.6
May	5	5.0	1.6	2.4	4.2
June	2	6.8	5.5	5.7	6.8
July	4	11.8	4.6	5.5	8.6
August	2	15.1	11.0	...	13.0
September	3	11.0	7.8	10.9	9.4
October	2	27.4	11.2	11.2	27.4[a]
November	1	17.8	14.3	14.3	17.8
1946					
May	2	5.6	2.4	2.8	4.0
June	1	5.0	2.5	2.5	5.0
July	1	5.2	3.2	3.2	5.2
August	5	16.0	8.3	...	11.7
September	2	17.0	14.1	...	15.5
1947					
January	2	13.6	9.3	12.5	11.4
March	1	10.6	7.3	7.3	10.6
April	1	8.0	6.4	6.4	8.0
June	2	6.9	2.7	3.1	4.9
July	2	10.8	8.5	...	9.7
August	3	11.2	10.3	...	10.8
October	1	8.5	4.3	4.3	8.5
November	2	8.2	6.2	8.2	6.2
1948					
June	4	8.1	3.1	4.0	7.0
July	7	13.9	3.8	3.8	11.0
August	2	15.5	13.7	...	14.6
October	1	7.6	5.5	7.6	5.5
November	1	8.7	8.7	...	8.7

[a]High value; fish from Harbour du Loutre.

TABLE IV (continued)

Month and year	Number of samples	Highest fat content	Lowest fat content	Average fat content	
				7.0–14.0 cm.	14.5 cm and up
		%	%	%	%
1949					
April	2	4.9	4.5	4.7	4.7
June	1	6.3	5.6	...	6.0
July	2	11.6	3.8	4.4	8.8
August	2	12.8	8.6	...	10.7
September	3	7.8	2.6	3.2	7.8
October	1	5.1	5.0	5.0	5.1
November	2	4.5	1.6	2.1	4.5
1950					
May	3	6.5	1.3	4.4	3.9
June	3	13.2	8.5	8.8	11.0
July	3	13.6	8.2	...	10.5
August	5	14.9	8.3	...	10.6
September	2	12.7	3.6	3.6	10.5
October	1	10.0	10.0	...	10.0
1951					
August	1	16.3	16.3	...	16.3
September	1	10.2	7.5	7.5	10.2
November	1	5.8	5.2	5.8	5.2
1952					
February	2	5.8	4.3	5.4	5.0
July	3	10.2	5.1	...	7.3

The trend of the average fat content for all sizes of "sardine" herring is shown graphically in Fig. 1.

There are general similarities in the picture presented by each year but there is much variation. Table IV supports the conclusion that the larger fish are fatter, with a few exceptions. Not all of the apparent exceptions contradict this statement. In some months individual samples all conformed but one particularly fat sample of small fish, with no admixture of large ones, occasionally reversed the usual order.

Unfortunately pressure of other work prevented adequate winter sampling after 1945. The winter of 1942–43 appears to be unique, as has been mentioned above. The herring were very fat from December to March (14 to 20%). In the following winter of 1943–44 the fat content was under 10%. In the sardine factories tables and machines were dripping oil in the 1942–43 winter, while iron parts tended to rust in the following winter.

It was thought that there might be a connection between this winter fatness and the abundance of plankton in the late summer and fall preceding. Plankton samples were collected monthly at *Prince* Station 5 between Campobello Island and the Wolves and more frequently at *Prince* Station 6 in the mouth of the St. Croix River. Because of wartime conditions and lack of usual boats no winter tows were taken.

The displaced volumes of food in vertical tows from 90 to 0 metres, at *Prince* Station 5, are shown in Fig. 2 for the period from June to November,

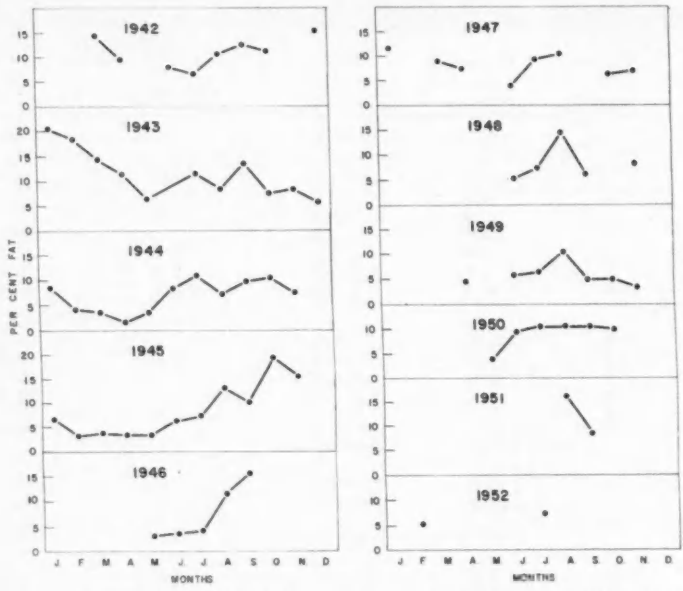

FIG. 1. Fatness of Bay of Fundy herring by months for the years 1942 to 1952.

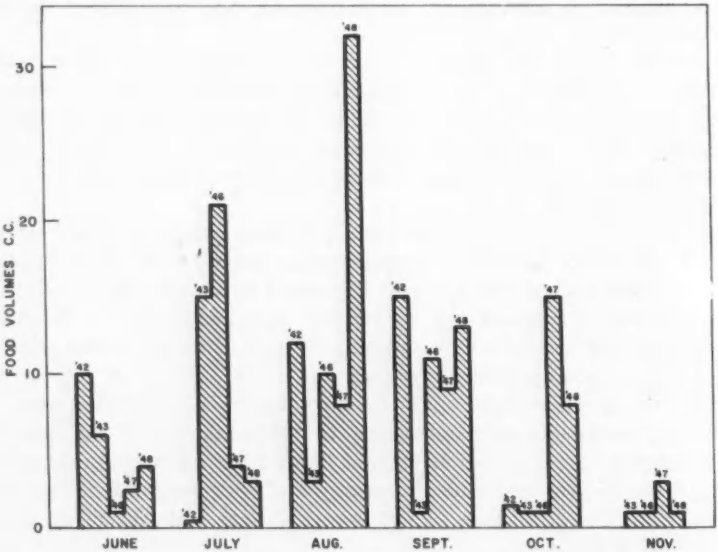

FIG. 2. Displaced volume of planktonic food in vertical tows (90 to 0 metres) from *Prince* Station 5, June to November, 1942, 1943, 1946 to 1948.

1942–1948. The year 1942 was more productive than 1943 in every month except July. However, plankton production in October and November was very low in each of these years as compared to 1947 and 1948, years in which the fat content of the herring does not seem, from limited data, to have been at all unusual. Dominant species in the plankton were similar in both years.

At *Prince* Station 6 the quantity of plankton in vertical hauls was equal in 1942 and 1943 in August and November but greater in 1942 in September and October.

(c) Variation of Fatness with Locality

Examination of the records indicates that herring from Harbour du Loutre, Campobello Island, were always very fat in comparison with those from other sources. A few examples are: June 12, 1942—12.7%; September 3, 1943—large 19.4%, small 14.8%; June 19, 1944—large 14.5%, small 12.2%; June 21, 1944—large 15.5%, small 10.0%; October 19, 1945—27.4%. These findings agree with the fishermen's contention that Harbour du Loutre herring make the finest bait for groundfish.

Elsewhere the fat content varies much from sample to sample and no particular order is apparent. No significant differences were seen within Passamaquoddy Bay as is shown by the following example:

Perry Shore, Maine	June 9, 1943	8.1% fat
Navy Island, N.B.	June 5, 1943	6.8% "
Oak Bay, N.B.	May 26, 1943	7.7% "

A month later Perry shore fish were showing over 10% fat, while eastern Passamaquoddy Bay fish were around 5%. Some time later the situation was reversed.

(d) Variation of Fatness with Disease

Very little was done to compare fish that showed symptoms of the fungus disease (*Ichthyosporidium hoferi*) with normal ones. Only three cases can be reported; in each case uniform-sized fish were compared.

Bocabec, N.B.	November 14, 1951	normal	6.7% fat
		diseased	4.9% "
Pocologan, N.B.	February 7, 1952	normal	4.7% "
		diseased	5.2% "
Maces Bay, N.B.	February 25, 1952	normal	6.3% "
		diseased	5.4% "

These diseased herring were recovering and no marked effect of the disease on fatness is indicated.

DISCUSSION

Earlier work, reported by Battle *et al.* (1936), agrees in many respects with the present results. They used the condition factor and opinions of fishermen to arrive at an estimate of fatness. Actual measurements were confined to a few months of one year, 1933.

They found that the condition factor improved with size from 10 to 23 cm. length. The present results, on the basis of fat determinations, show a much steeper rise, as would be expected.

Present results agree with theirs concerning the exceptional fatness of herring at Campobello Island, and, in particular, in Harbour du Loutre. However, I did not find such consistently poor fish as they reported on the western side of Passamaquoddy Bay on the Perry shore in Maine.

Differences in fatness of herring caught at individual weirs, over short time intervals, indicate that the schools are moving about, as recent tagging also shows (McKenzie and Tibbo, 1958). Herring must remain in the Harbour du Loutre region long enough to become quite fat.

The difference in fatness of the herring in the winters of 1942–43 and 1943–44 has been referred to above. The abundance of the plankton was also reported, since herring feed directly on it. Some other possible factors are now discussed.

The annual mean surface water temperature at St. Andrews, New Brunswick, and at Portland, Maine, was average in 1942 and a little below average in 1943. Considerably higher temperatures occurred in 1946 and 1947 (Hachey and McLellan, 1948). Various authors have stated that high plankton content of the water is usually associated with low temperature (Herdman, 1923, pages 258–261). Such a relation does not hold here as the warmest years also had the most plankton.

No significant differences are apparent in river run-off for 1942 and 1943, as measured for the Saint John River (Dominion Water and Power Bureau, 1948, 1949; Water Resources Division, 1951). Run-off was higher in 1946 and 1947, a factor that may be associated, through nutrient salts, with the plankton production of those years.

These factors are reported here for possible integration when more is known of their interaction in the economy of the sea. They do not appear to explain the very fat herring of December 1942 to March 1943.

SUMMARY

1. Fat determinations, by ether extraction, are reported for 205 samples of "sardine" herring (*Clupea harengus* L.) from the Quoddy region, collected from March 1942 to July 1952. The most consistent year-around coverage was in 1942–1945.

2. Within a sample the larger fish were fattest, until sexual maturity was reached.

3. The fish were poorest from April to June inclusive, and fattest from August to November, also inclusive.

4. The highest fat value found was 27.5% of the wet weight of the fish and the poorest was 1.2% of the wet weight.

5. Fish from Campobello Island and particularly from Harbour du Loutre, New Brunswick, were very fat, exceeding those from other parts of the region.

6. The winter of 1942–43 was noted for exceptionally fat "sardines". There is a degree of correspondence with more abundant plankton in the late summer and autumn of 1942. In subsequent years this relation broke down.

7. There was much yearly variation in fat content of the fish and much local variation in short periods of time. The latter indicates considerable movement of the schools of fish.

8. *Ichthyosporidium* disease had little effect on the fatness but depressed it somewhat.

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Miss Fae Hallett and Miss Phyllis J. Gibson made most of the fat determinations in the laboratory. Mr. J. E. Henri Legare and Mrs. Delphine C. Maclellan examined the plankton from *Prince* Stations 5 and 6. Mr. S. N. Tibbo provided information on physical factors. Mr. L. R. Day read the manuscript and offered constructive help. To all of these persons special thanks are proffered.

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On the Biology and Fishery of the Canadian Atlantic Halibut, *Hippoglossus hippoglossus* L.[1,2]

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ABSTRACT

Exploratory fishing in the northern Gulf of St. Lawrence in 1945 and 1946 and off western Nova Scotia in 1947 caught 739 halibut, of which 229 were tagged and released. About 590 fish from the commercial fishery of the two regions were also examined.

Larger, older halibut were caught in the northern part of the Gulf of St. Lawrence than off western Nova Scotia. Tagged halibut recaptures, size and age composition of commercial landings, and differences in rate of growth suggest generally separate stocks in the two regions.

Younger, immature halibut were most available in shallower water; larger, mature fish usually in deep water. Most halibut were caught at temperatures between about 3° and 9°C. Seasonal, inshore, relatively shallow water halibut fisheries in the northern part of the Gulf of St. Lawrence and off western Nova Scotia occur as the bottom water warms. Large female halibut predominate in such catches.

Mature halibut, about 9 to 11 years and older, must spawn in late winter and early spring, probably along the deep-water edge of the banks. Mature halibut grow slowly though the females exceed the mature males and reach a much larger size. The faster-growing, immature halibut of both sexes grow at about the same rate.

Halibut landings from ICNAF Subareas 3 and 4 which were at a low level between 1940 to 1948 increased sharply to about 13 million pounds in 1950. More recent landings approximate the long-term annual average of about 5 million pounds. Changes in the level of landings are related to changes in the magnitude of the Canadian fishery which, since 1940, has produced most of the halibut from Subareas 3 and 4.

Offshore and inshore fisheries specifically for large halibut produce most of the landings. Catches of halibut taken incidentally in other fisheries contribute little by weight but take large numbers of small, faster-growing individuals. With a continuation of present fishing practices and intensities an annual yield of about 5 million pounds may be expected to continue, but some increased yield might result from controlling the incidental catches of younger halibut. Ways and means of effecting such control should be explored.

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INTRODUCTION

THE FISHERY FOR HALIBUT on grounds off the Canadian Atlantic coast began about 100 years ago (Bigelow and Schroeder, 1953). At that time it was prosecuted by United States vessels. Canadian fishermen were little interested in this species until about the end of the nineteenth century, but since that time halibut, the highest priced groundfish species, has been sought after.

In 1954 total halibut landings from the northwest Atlantic, the banks and fishing grounds off the east coasts of New England and Canada, and the west coast of Greenland, were about 8 million pounds, eviscerated weight, head on. Approximately 70% of this total came from banks off the Canadian mainland and Newfoundland, with most of the remainder from the fishing grounds off Greenland. Canadian vessels caught about 97% of the halibut landings from the banks off Canada and Newfoundland.

Unlike the North American fishery for Pacific halibut, *Hippoglossus stenolepis*, landings from the northwest Atlantic have never been regulated. On the Pacific coast halibut landings between 1946–54 averaged about 65 million eviscerated, head on pounds annually, while northwest Atlantic landings averaged about 5½ million eviscerated, head on pounds annually. Because the Pacific coast fishery is so important, knowledge and conservation of the halibut stocks there have been the object of study by an international commission. In contrast, our knowledge of the halibut of the northwest Atlantic is slight. McKenzie (1946) has described Canadian fishing methods and the grounds fished. Bigelow and Schroeder (1953) give a general account of the halibut in northwest Atlantic waters, based mainly on accounts of the halibut's life-history in European waters and that of the related species (*H. stenolepis*) in Pacific waters. The current study adds to limited knowledge of the halibut's distribution and life-history in the Canadian Atlantic region.

In 1944 experimental fishing for halibut was initiated in the Gulf of St. Lawrence by the Fisheries Research Board of Canada. During 1946 and 1947 a more detailed study of the life-history and movements of the halibut was carried out. At that time the halibut fishery was at a low level. Landings were mainly from two inshore fisheries, one in the northern part of the Gulf of St. Lawrence, the other off western Nova Scotia. Exploratory fishing was carried out in these two regions using the M.V. *J. J. Cowie*. A total of 229 halibut were tagged in both areas. About 510 halibut caught in exploratory fishing were measured and examined, as were 590 fish taken in the commercial fishery of both regions. While only 1,325 halibut were tagged and examined, they provide useful information about the halibut in these regions. Analysis of the commercial fishery statistics also provides information about the stocks of halibut in northwest Atlantic waters.

METHODS AND MATERIALS

FISHING METHODS

Hook and line gear was used to catch all halibut, both in exploratory fishing and for tagging. The *J. J. Cowie* was rigged in the style of the Pacific coast

longliner, with a chute to set the longline gear and a gurdy to haul it aboard. The hooks were attached at approximately 2-fathom intervals along a groundline which was set on the bottom in strings up to 2 or 3 miles long. Each string was made up from lines (50-fathom units) which are used as the unit of effort in this paper. The groundlines, of 40–48 lb. tarred cotton, gangings of 13–14 lb. tarred cotton, and #6284 Mustad hooks used were much larger than those used for cod and haddock fishing. The period of time the gear was allowed to remain on the bottom, known as the "soak", varied from 3 hours to overnight during exploratory fishing. While tagging, the soak was never more than 5 hours. (For a description of halibut fishing methods and gear, see Thompson and Freeman, 1930).

Tagging Methods

Halibut were tagged with monel metal strap tags attached to the operculum near its upper margin. The tag, method of attachment, and region of attachment were essentially as described for the Pacific halibut by Thompson and Herrington (1930). Only vigorous, lightly hooked halibut were tagged and about three quarters of those caught could be placed in this category. Prior to tagging, the fork length of the halibut was measured to the nearest centimetre. Date, tag number, length, place of release, and depth were recorded for each halibut tagged.

Biological Observations

All halibut caught were measured, and those not tagged were measured and weighed. In 1946 some meristic counts, pectoral fin lengths, and head lengths were taken from these and also from those examined in the commercial catch. Definitions of these measurements are as follows:

FORK LENGTH. The length in centimetres from the tip of the closed lower jaw to the distal end of the middle part of the tail was taken to the nearest centimetre.

ROUND WEIGHT. Weight of the whole fish, in all cases weighed at sea with a beam balance suspended from the boom of the vessel.

EVISCERATED WEIGHT. Weight of the fish after removal of viscera, gonads, and gills. Most of the halibut examined from the commercial landings had been eviscerated previously.

HEAD LENGTH. Recorded to the nearest millimetre from the tip of the snout to the end of the operculum, but not including the flap at the posterior end of the operculum.

PECTORAL FIN LENGTHS. From the insertion of the fin to the tip of the longest fin ray recorded to the nearest millimetre.

MERISTIC COUNTS. The total number of fin rays in the dorsal and anal fins.

In addition, coloration of halibut was noted, particularly that of the white or left side. Sex and stage of gonad development were recorded for most of the halibut examined at sea during 1946 and 1947. Otoliths were removed for age determination from samples of the catch.

Age Determination Method

Otoliths were used for age determination. They were preserved in a 50% glycerin solution with a few crystals of thymol added as a preservative. The otoliths were read without breaking, grinding, or polishing. For examination, an otolith was placed in glycerin solution and examined under a binocular microscope (6×) using reflected light against a dark background. An opaque and transparent zone together were considered to represent one year's growth. All otoliths were read at least twice, and, because many of the specimens were old fish, the otoliths were difficult to read. Most difficulties arose in the interpretation of the annual rings. Some old fish, even 20 years and more, had good otoliths which could be read with little doubt. Others had many closely grouped rings toward the edge and these had to be interpreted according to their pattern. There is thus a subjective element in the age determination of these halibut.

Sources of Statistics

Canadian landings for 1920 to 1951 were obtained from Fisheries Statistics of Canada. United States landings for the same period were obtained from Fishery Statistics of the United States. After 1951 total landings were obtained from the Statistical Bulletin of the International Commission for the Northwest Atlantic Fisheries (ICNAF). Canadian landings of each species of groundfish for individual trips by each vessel have been recorded by the Department of Fisheries, for otter trawlers since 1930, and for dory vessels since 1941. Log records giving effort and area fished have been collected from a representative number of the otter trawl and dory vessel fleet since 1948 by the Fisheries Research Board of Canada. Both these sources have been used to obtain catch-per-unit-of-effort data and area fished.

All weights reported in the statistics of landings throughout this paper refer to gutted weight, head on. Where necessary, conversion factors have been used to bring weights as reported by various sources to a common unit (round weight multiplied by 0.83 or head-off weight multiplied by 1.15 equals head on, gutted weight).

For convenience the ICNAF subareas and subdivisions are often used to denote the various fishing regions, as shown in Fig. 1.

LOCATION OF FISHING GROUNDS AND MOVEMENTS OF FISH

General Location of Halibut Fishing Grounds

Important halibut fishing grounds occur in both Subareas 3 and 4. In 1953 and 1954 the greatest landings from Subarea 4 came from grounds off western Nova Scotia, ICNAF Subdivisions 4X and 4W (Fig. 1). For Subarea 3 the most important grounds are located in Subdivisions 3P and 3O. The Gulf of St. Lawrence region is much less important, with most landings there taken from Subdivision 4S. In 1951 and 1952 Subdivision 4V produced large landings. McKenzie (1946) has presented the distribution of halibut catches for 1938–40. The distribution of catches then is similar to that of 1953–54; although both Subarea 3

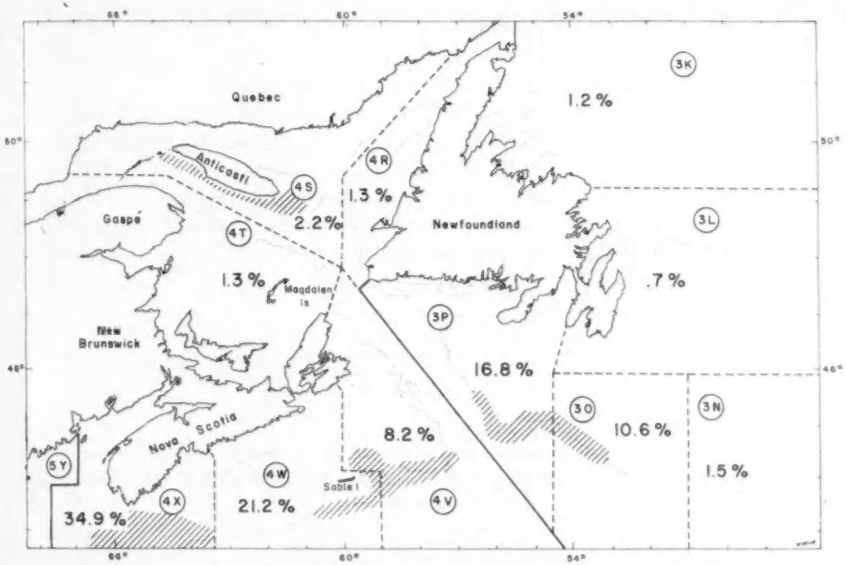

FIG. 1. Percentage of halibut landings taken in 1953–54 from each sub-division of Subareas 3 and 4. Important fishing grounds denoted by cross hatching. The dotted line is the 100-fathom contour.

and the Gulf of St. Lawrence were of slightly greater importance in 1938–40 than they were in 1953–54, while Subdivision 4W was of lesser importance. The comparison suggests that the halibut fishing grounds have not changed significantly. However, their relative importance fluctuates from year to year. The increased importance of Subdivision 4W probably results from the development of medium-sized longliners in western Nova Scotia and increased effort in that region.

Within the various subdivisions the halibut fishing grounds are localized. Log records for large dory vessels show that in Subdivisions 3O, 3P, and 4V, all fishing for halibut was carried out along the 100-fathom contour. In Subdivisions 4W and 4X most of the landings were made by small and medium longliners. Although records of their activities are less precise than for the large vessels, they show that many of these operated at depths of 100 fathoms or more. In Subdivision 4X, however, a late summer fishery in relatively shallow water (about 30-70 fathoms) off the southwestern tip of Nova Scotia contributes heavily to the landings in this Subdivision.

Movements and Distribution in the Northern Gulf of St. Lawrence

FROM TAGGING. In June, 1946, 75 halibut were tagged and released in deep water (95-125 fathoms) southwest of Anticosti Island in the northern portion of the Gulf of St. Lawrence (Fig. 2). Length frequencies of the tagged and recaptured halibut are presented in Table I.

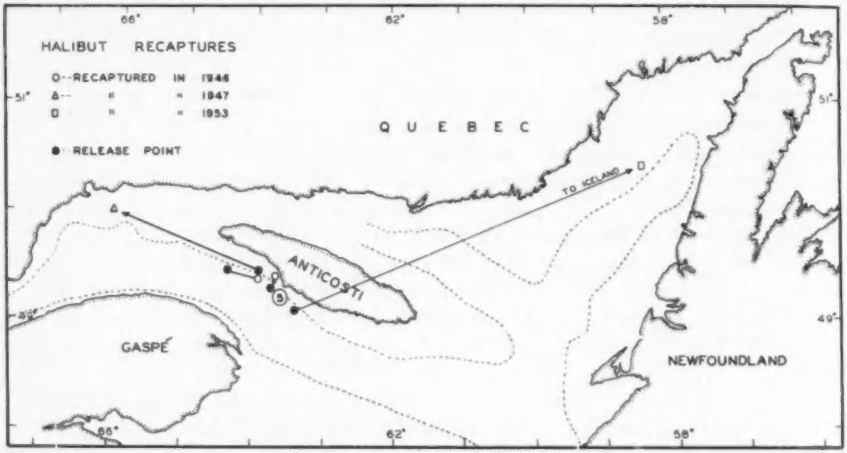

FIG. 2. Recaptures from 75 halibut tagged in June, 1946, southwest of Anticosti Island in the Gulf of St. Lawrence.

TABLE I. Length frequency for mid-20 cm. length classes of halibut tagged off Anticosti Island in 1946, and of halibut recaptured 1946–53. Recaptured halibut are grouped according to length at time of tagging.

Mid-class length *cm.*	72.5	92.5	112.5	132.5	152.5	172.5	192.5	Total
	no.	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*
Tagged	1	3	9	17	27	9	9	75
Recaptured	...	...	2	2	3	1	1	8

Nine halibut, 12%, have been recovered from the Anticosti tagging. Seven of these were recaptured in the summer months of the tagging year, and 1 in 1947, the year following tagging (Martin and McCracken, 1950). These 8 were recaptured in the Gulf of St. Lawrence, and, in general, close to the tagging region. None were from the banks off Nova Scotia or Newfoundland or from the shallower waters on the Gaspé side of the deep-water Laurentian Channel. While 8 of the 9 recoveries suggest a local stock with limited movements, it is difficult to suggest that distance or depth is a barrier since 1 of these tagged halibut was recovered off Iceland in 1953 (McCracken and Martin, 1955).

Only 2 halibut tags were returned from the commericial fishery in the Gulf of St. Lawrence. The others were taken during exploratory fishing in the months following tagging, mainly from deep water off Southwest Point, Anticosti Island, where no other vessels were operating. The nearest commercial fisheries were in shallow water 60–80 miles away from the tagging region. Low returns from the commercial fishery probably reflect limited movement by these halibut. The results, however, suggest that some halibut tagged in deep water in spring move into shallow water during summer, while others remain in the deep water.

Seasonal Distribution of Commercial Catches

The commercial fishery for halibut in the Gulf of St. Lawrence is seasonal. From observations in 1946 the fishery was mainly in July and August (Table II) by small inshore boats using hand hauling. These were fishing in relatively shallow water, about 50 fathoms or less, mainly off the southeastern end of Anticosti Island and along the Quebec shore between Seven Islands and Natashkwan. Commercial fishing effort reached a maximum in July and August. Both earlier and later in the season effort was low because halibut were said to be unavailable in shallow water, also handlining and hauling longlines by hand are difficult from the deep water.

Table II. Monthly landings of halibut in Quebec by the commercial fishery during 1946, in hundreds of pounds.

Month	Landings
	cwt.
May	5
June	165
July	767
August	606
September	95
October	36
November	7
Total	1,681

In contrast, exploratory fishing produced generally better catches in June and September (Table III). Catch per line was usually highest then and generally better in deep water than shallow throughout the season. In 1944 and 1945 halibut were taken in shallow water as early as the end of June. No halibut fishing was carried out in shallow water earlier. In 1946 halibut were still present in shallow water in September.

Halibut appeared to be most abundant in deep water in spring and again in early fall, and their availability in shallow water increased in summer. The results suggest that part of the stock found in deep water in spring moves into shallow water in summer. However, lack of fishing in shallow water in spring precludes a definite conclusion that halibut are absent from the shallows then.

Size Composition by Depth

Halibut caught by exploratory fishing from deep water southwest of Anticosti Island ranged from about 60 to 235 cm. in length (Fig. 3). Their modal size frequency was between 130 and 160 cm. In contrast, commercial landings from shallow water had more small and very large fish. The modal size of fish taken by commercial fishermen off Heath Point, Anticosti, July 26–Aug. 3, was about 200 cm. in length. Their landings also included more small fish than those from deep water. Selection by the halibut gear may have reduced the numbers of both small and large fish taken in deep water (i.e., the hooks may have been too large to take small fish and some large fish may have broken loose in hauling from deep

TABLE III. Total catch and catch per line for Anticosti regions from records of the motor vessel *J. J. Cowie.*

Year	Date	Depth	Lines fished	Catch	Catch per line
		fathoms	*no.*	*lb.*	*lb.*
1944	May 31–June 19	75–110	2046	32,900	16.1
	June 30–July 6	9–14	102	600	5.9
	June 30–July 6	80–105	840	7,300	8.7
			2988	40,800	Av. 13.7
1945	May 26–June 3	85–130	540	2,400	4.4
	July 1–July 29	100–120	895	6,475	7.2
	July 1–July 29	8–20	880	5,500	6.2
			2315	14,735	Av. 6.2
1946	June 8–July 1	95–130	545	7,815	14.3
	June 8–July 1	60–75	65	0	0
	July 25–July 30	100–150	205	1,328	6.5
	July 25–July 30	10–85	100	115	1.2
	Sept. 3–Sept. 25	20–30	75	200	2.7
	Sept. 3–Sept. 25	100–135	725	1,108	15.3
			1715	20,566	Av. 12.0

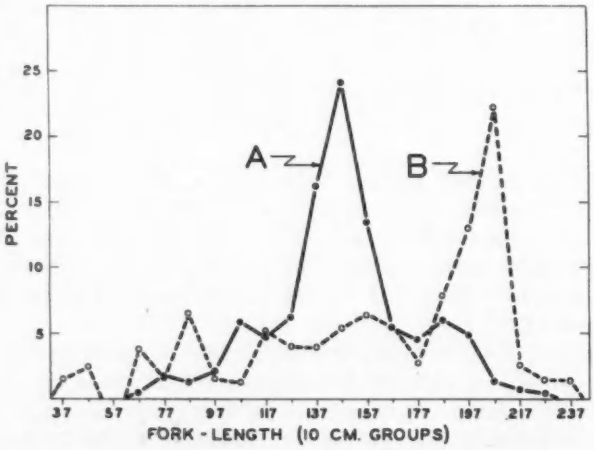

FIG. 3. Percentage size composition of halibut taken around Anticosti Island in 1946. A—deep-water, exploratory catches; B—shallow-water, commercial landings.

water). For intermediate sizes of halibut, gear selection should have been similar in both shallow and deep water. The size composition of the catches suggests that intermediate size halibut are numerous only in deep water throughout the summer.

DEPTH AND SEX RATIO

In May, 1945, catches of halibut from deep water along the north shore of Anticosti contained more females than males (Table IV). In July and September

of 1946 the males exceeded females in the deep water, the differences being substantial in the latter month. Numbers of halibut taken by exploratory fishing in shallow water are inadequate for similar analysis. However, large halibut in commercial catches from shallow water are believed to be mainly females. Although none could be sexed, since they had been gutted before landing, about 55% of the halibut measured were larger than the largest male seen during this study. It is believed that the population found in shallow water during summer has a high proportion of female halibut. The most plausible explanation is that they have moved there from the deeper, more offshore waters.

TABLE IV. Sex ratio of halibut caught off Anticosti in relation to depth and season.

	Depth and sex ratio					
	50 fathoms and less			Over 80 fathoms		
Season	Total	Male	Female	Total	Male	Female
	no.	%	%	*no.*	%	%
May 1945	...	...	...	31	42	58
July 1946	...	...	...	17	71	29
Sept. 1946	4	0	100	133	66	34

DISTRIBUTION WITH TEMPERATURE

Halibut were taken in quantities only where temperatures were above about 2.5°C. in any of the areas fished in the Gulf of St. Lawrence (Table V). Below 1.6°C. the catch was nil for both the Anticosti and Newfoundland areas. Between temperatures of 2.5°C. and 4.5°C. the catch per 50-fathom line ranged from 3 pounds to about 20 pounds.

Information obtained about catches at temperatures above 4.5°C. is limited. Fishermen were catching halibut from shallow water in July and August, probably at temperatures between 5° and 10°C.

MOVEMENTS AND DISTRIBUTION OFF WESTERN NOVA SCOTIA

FROM TAGGING. Between the end of April and mid July, 1947, 154 halibut were tagged and released off western Nova Scotia (Fig. 4). Tagging regions were more dispersed than in the Gulf of St. Lawrence and tagged halibut were released at depths from 30 to 200 fathoms. Length frequencies of tagged halibut and recaptured halibut are presented in Table VI. In general, they were smaller than those released in the Gulf of St. Lawrenc.

Twenty-three halibut recaptured by the commercial fishery have been reported, about 15% of those tagged. While most recaptures were made in the year following tagging, from 1 to 3 halibut have been recovered each year up to and including 1955, except in 1954.

Most of the tag recoveries have come from the western Nova Scotia region and show movements only over short distances. They indicate that halibut remain inside the edge of the continental shelf at all seasons. Four distant recoveries have

TABLE V. Availability of halibut related to temperature in the Gulf of St. Lawrence.

Month	Depth	Temperature	Lines set	Total weight	Weight per line
	fathoms	*°C.*	*no.*	*lb.*	*lb.*
SOUTHWEST POINT, ANTICOSTI ISLAND					
June	95–125	4.5 to 2.9°C.	290	5,957	20.5
July	95–125	4.2 to 2.4°C.	125	947	7.6
July	130–200	4.2 to 4.0°C.	100	653	6.5
July	10–20	1.4 to 9.9°C.	60	115	1.9
July	20–45	1.4 to −0.7°C.	20	0	0.0
July	60–85	1.6 to 0.0°C.	20	0	0.0
ELLIS BAY, ANTICOSTI ISLAND					
June	95–125	4.2 to 3.0°C.	165	1,296	7.9
June	60–75	0.9 to 0.2°C.	65	0	0.0
July	100–110	3.4 to 3.1°C.	15	180	12.0
July	130–140	...	15	110	7.3
POINTE RICHE, NEWFOUNDLAND					
May	100–130	4.0 to 2.8°C.	160	476	3.0
May	47–80	1.3 to 0.0°C.	25	0	0.0
August	100–123	...	40	0	0.0
August	125–153	4.5 to 4.3°C.	30	0	0.0
August	9–75	...	110	10	0.09
BAY OF ISLANDS, NEWFOUNDLAND					
May	115–125	4.5 to 3.1°C.	40	168	4.2

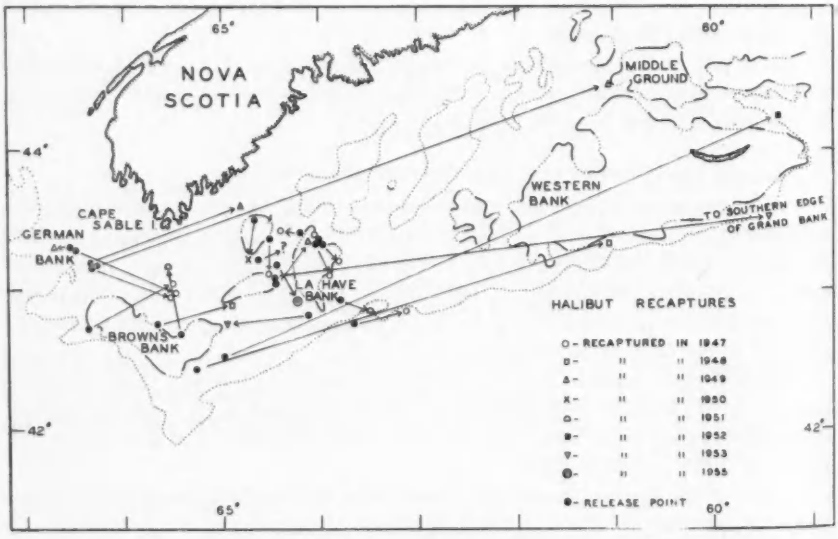

FIG. 4. Recaptures from 154 halibut tagged off western Nova Scotia in 1947.

TABLE VI. Length frequency for mid-20 cm. length classes of halibut tagged off western Nova Scotia in 1947, and of halibut recaptured 1947–55. Recaptured halibut are grouped according to length at time of tagging.

Mid-class length, *cm.*	52.5	72.5	92.5	112.5	132.5	152.5	172.5	Total
	no.	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*
Tagged	6	28	48	37	17	14	4	154
Recaptured	...	3	4	6	6	3	1	23

been made to the eastward of the tagging region. One halibut was recaptured on the southern edge of the Grand Banks, about 600 miles away.

Recaptures of halibut released in the LaHave–Roseway region indicate that the stocks of LaHave–Roseway and Baccaro Banks intermingle but remain distinct from other areas. Halibut recovered in the late summer fishery off Cape Sable Island came from German and Browns Banks rather than from the eastward.

Seasonal movements from deep to shallow water or the reverse are not apparent in this region from the tag recaptures. Halibut taken in relatively shallow water off Cape Sable came from about the same depths on banks to the westward.

SEASONAL DISTRIBUTION OF CATCHES

The commercial fishery for halibut off western Nova Scotia, Subdivision 4X, is carried out mainly by longliners 55 feet or less in length. The fishery is seasonal, with most of the landings occurring between May and October (Table VII). Principal landing ports in the eastern part of this region are Lockeport, Liverpool, Port LaTour and Shelburne. At Liverpool, where records of individual trips have been collected, longliners fishing haddock and cod turn to halibut fishing in April and May and continue until October. Most of these halibut are caught well offshore in the deep water beyond LaHave Bank (some catches are made in deep

TABLE VII. Halibut landings off western Nova Scotia, by months and regions in 1953.

Month	East of Cape Sable (Queens to Shelburne Co.)	Cape Sable (Shelburne West)	West of Cape Sable Yarmouth to (Digby Neck)	Total
	cwt.	*cwt.*	*cwt.*	*cwt.*
January	33	2	41	76
February	45	2	31	78
March	75	1	142	218
April	113	...	348	481
May	600	78	115	793
June	1,067	147	169	1,383
July	1,332	395	79	1,806
August	1,236	1,723	57	3,016
September	744	2,075	121	2,940
October	967	2,230	37	3,234
November	341	4	10	355
December	92	1	13	106
Total	6,665	6,658	1,163	14,486

water off Emerald Bank and Sable Island Bank, Subdivision 4W). That effort ceases in fall and winter seems related to weather and distance from shore rather than reduced availability of halibut. Boats from the other major ports follow a similar fishing pattern.

West of Cape Sable the halibut fishery is of less importance. However, peak landings occur there between March and June. Interviews with local fishermen indicate that these halibut are being taken from depths of about 50 to 60 fathoms on grounds off the tip of Digby Neck and Lurcher Shoals. It is also known that some of the larger longliners, particularly from Yarmouth, fish on Browns Bank and German Bank in the early summer.

Off Cape Sable landings are concentrated between August and October. Numerous small longliners fish on grounds in an arc extending from about southeast to southwest of the Cape. Depths fished range from about 35 to 80 fathoms. Local fishermen claim that halibut are not available on these grounds in attractive quantities earlier than late July. However, cessation of the fishery in October may not be related to decreased availability of halibut. Inclement weather makes the fishery less attractive, and in addition, preparations for the December 1st opening of the lobster season begin in early November.

The timing and distribution of commercial catches suggest a seasonal concentration of halibut in fairly shallow water off Cape Sable Island. Tagging results suggest that these halibut come mainly from grounds to the west, German and Browns Banks, and probably from the same depths. The pattern of the commercial fishery supports this suggestion, since on grounds to the west of Cape Sable halibut catches were high in spring but reduced during late summer and early fall when catches were at a peak in the Cape Sable region (Table VII).

Distribution of Exploratory Catches

Catches by the *J. J. Cowie* in exploratory halibut fishing off western Nova Scotia in 1947 also help to clarify the pattern of halibut movements in that region. Fishing was carried out between April and October (interrupted between mid July and mid August) from German Bank to LaHave and Roseway Banks. Catches of halibut were made throughout the area (Fig. 5). Good catches were made throughout this period at depths over 100 fathoms off LaHave Bank. Around LaHave Bank and between Roseway and LaHave Banks, between 50 and 100 fathoms, catches were generally better between June to October than in April to May. To the west, catches were best around German Bank in June to July, and poor in April to May and August to October. Off Cape Sable catches were good only in the August to October period. It may be noted that in late October, two sets off Cape Sable failed to produce any halibut.

Exploratory catches suggest that halibut moved into the intermediate depths around LaHave and Roseway Banks by June. Possibly they came from deeper water. Good catches were made around German Bank in June to July, but declined later in the season as halibut catches were beginning off Cape Sable Island. Support is added to the result of the tagging which showed fish moving from the vicinity of German Bank to Cape Sable grounds.

Size Composition by Depth and Area

In the LaHave–Roseway Bank region experimental fishing was carried out from depths under 50 fathoms to over 100 fathoms. Small fish (under 75 cm.) were missing from the catch at depths over 100 fathoms (Fig. 6). Even the medium-sized fish (76-100 cm.) were of reduced importance in the catch, and those caught tended to be near the upper limit of this size range. Large halibut, over 100 cm., predominated in the catches. Small, medium, and large fish were taken in shallower water, particularly on top of the banks (under 50 fathoms) and along the edges of the bank. That large- and medium-sized fish tended to be of greater importance than small fish seems related to the effect of gear selection.

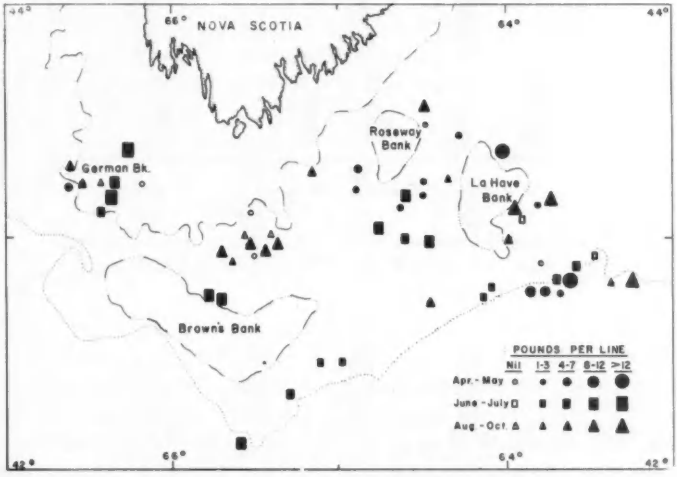

Fig. 5. Catch per unit effort of halibut off western Nova Scotia as shown by exploratory fishing of the *J. J. Cowie* in 1947.

In the Browns Bank–Cape Sable region small fish were also missing from the few deep-water catches (Fig. 6), and halibut were not taken at depths less than 50 fathoms. In the intermediate depths all three size categories of halibut were represented and the size composition of the halibut taken was similar to that at equivalent depths in the LaHave–Roseway region.

In the German Bank region halibut were not fished for in deep water, over 100 fathoms. In early spring large, medium, and small halibut were available but only at depths less than 50 fathoms (Fig. 6). Large fish made up the greatest proportions of the catch. In September to October only small and medium halibut were taken there, with small fish most important in the catch. This seasonal change in size composition suggests that large halibut had moved out of the German Bank region by late summer.

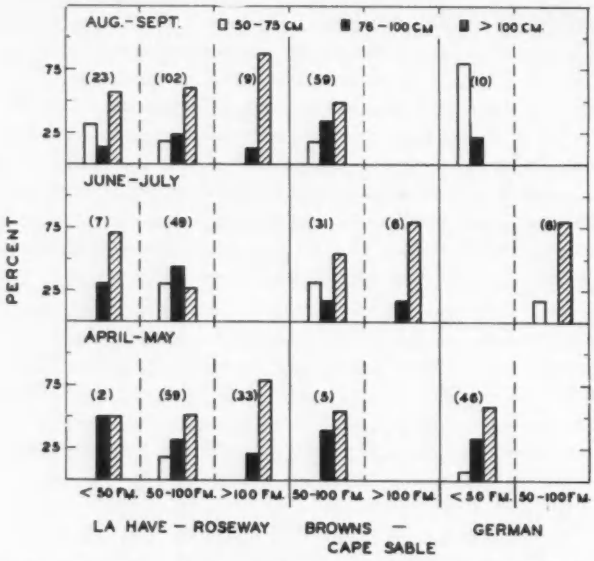

FIG. 6. Percentage size composition of halibut in relation to depth off western Nova Scotia. (Numbers of fish in parentheses.)

SEX RATIO AND DEPTH

In deep water, over 100 fathoms, large male fish were dominant in the catch (Fig. 7). At all other depths large female fish were much more numerous than large males. Predominance of large females might be expected on the basis of growth rates. Sex ratios of medium and small fish tended to be nearly equal in shallow and intermediate depths, although there were differences between areas. In the LaHave–Roseway region medium and small male fish were more numerous than females, while in the Browns–Cape Sable and German Banks region females were more numerous than males. These differences tend to confirm the view that stocks of the LaHave–Roseway region do not intermingle with those of the other two regions. The results also suggest that there may be different behaviour patterns for large male and female fish.

DISTRIBUTION WITH TEMPERATURE

Off western Nova Scotia depths with water temperatures less than 3°C. were not fished for halibut to any extent. In the LaHave–Roseway regions bottom temperatures on top of the banks ranged from about 2.5°C. in April to 8°C. in September. Between 51 and 80 fathoms, where most of the halibut fishery was carried on, bottom temperatures ranged from about 3.5°C. in spring to about 9°C. in September. Good halibut catches were made there throughout this period. During the same period, good halibut catches were made in depths over 100

fathoms where temperatures ranged from about 8° to 11°C. Little change in availability of halibut is apparent within these seasonal temperature ranges.

It is difficult to assess whether or not temperature plays an important part in affecting the distribution of halibut in the Cape Sable and German Bank region. Water temperatures taken from May to October, 1947, indicate that the body of water in the Cape Sable Island region is not so thoroughly mixed as that of the

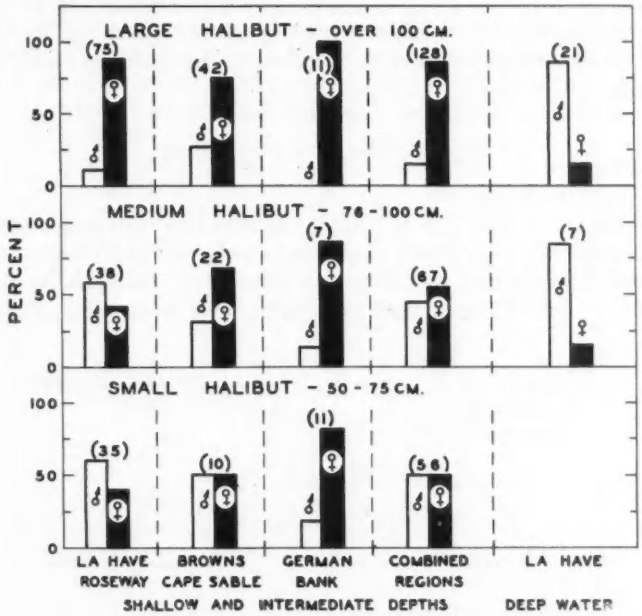

FIG. 7. Percentage male (♂) and female (♀) halibut by area, size and depth. (Numbers of fish in parentheses.)

German Bank region, but much more so than that of the LaHave–Roseway area. Waters at the bottom (about 40–60 fathoms) warm up slowly in the Cape Sable region and bottom temperatures comparable with those of German Bank in late May were not reached until late July. The halibut fishing season off Cape Sable Island is coincident with the period of relatively high temperatures.

It should be noted, however, that in the Cape Sable region in June bottom temperatures were about 5°C. The fishery there did not begin until temperatures were about 7° to 8°C. In the German Bank region catches were good with bottom temperatures at about 6° to 7°C., but poor, with only small fish taken, at temperatures of about 9° to 13°C. However, the range of temperatures in these areas does not exceed that at which halibut were found in the LaHave–Roseway area.

The distribution of halibut with temperature in the northern Gulf of St. Lawrence and off western Nova Scotia agrees closely with the distribution reported for other regions. Thus, Thompson and Van Cleve (1936) show that in both the Atlantic and Pacific Oceans the commercial fishery for halibut conforms in general to distributions of temperatures between 3°C. and 8°C. Jespersen (1925) reports that, off Greenland, halibut were found in depths with bottom temperatures of about 3°C. Jensen (1925) relates the movements of halibut into shallow water off Greenland to the warming of the water on top of the banks. The regions in which large halibut occur in shallow water off western Nova Scotia and in the northern part of the Gulf of St. Lawrence are areas of marked tidal mixing.

COMPARISON OF POPULATIONS

Size Composition of Catches

While the size composition of halibut catches varies with depth and possibly season, there are very real differences between catches in the Gulf of St. Lawrence and off western Nova Scotia. A much greater proportion of large halibut are caught in the Anticosti Island region than in western Nova Scotia (Fig. 8A and 8B).

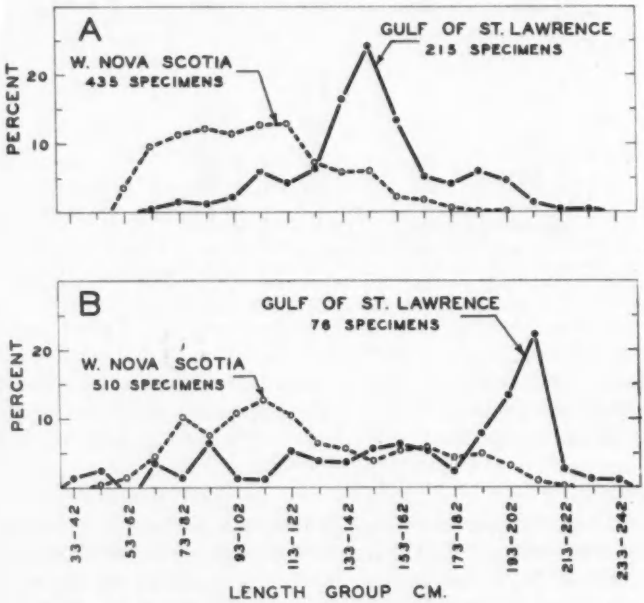

Fig. 8. Length composition of halibut from the northern part of the Gulf of St. Lawrence (1946) and western Nova Scotia (1947).
A. Experimental catches
B. Commercial landings

Both commercial landings and experimental catches show this feature. Modal size of commercial halibut landings from the eastern part of the Anticosti Island grounds was around 200 cm. (Fig. 8B). Few halibut of this size were taken off Nova Scotia. Although sizes ranged from about 50 cm. to over 200 cm., most fish were between 75 and 125 cm. in length.

Modal length of halibut in experimental catches off Anticosti, mainly from deep water, was between 125 to 165 cm. (Fig. 8A). Most catches of halibut with similar gear off western Nova Scotia had modes between 75 and 125 cm. in length.

Comparison of the size composition by sexes for the two regions shows striking differences (Fig. 9). Few males taken off western Nova Scotia were as large as the modal size of males off Anticosti Island. Similarly, female halibut off Anticosti Island were numerous at about 200 cm., a size seldom seen in the catches off western Nova Scotia.

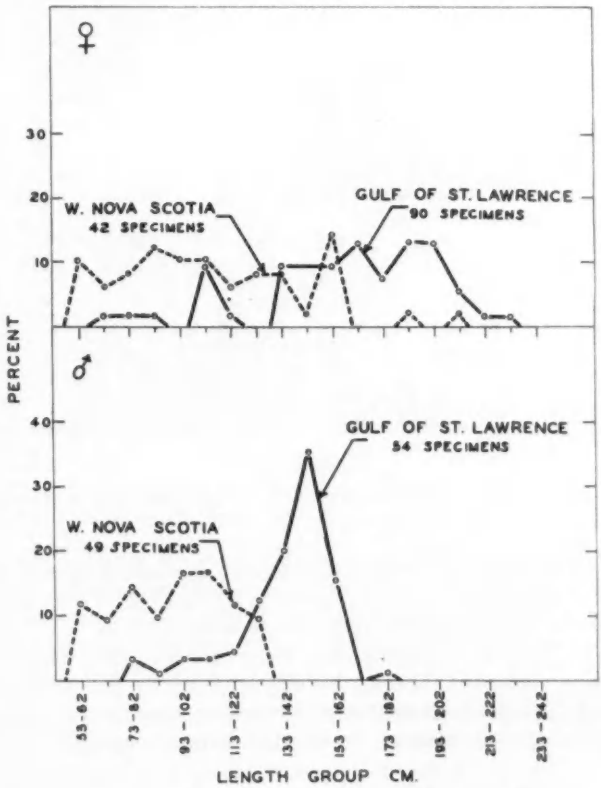

FIG. 9. Length composition of female (♀) and male (♂) halibut in experimental catches from the northern part of the Gulf of St. Lawrence (1946) and western Nova Scotia (1947).

Off western Nova Scotia tagging results suggest that stocks of halibut in the LaHave–Roseway region and the Cape Sable Island–German Bank region are relatively discrete. However, size composition of the halibut from the two regions is similar.

Age Composition

Age composition for halibut off Anticosti Island and western Nova Scotia is consistent with their size composition. Many more old halibut were taken in the Gulf (Fig. 10). Most of the halibut in the experimental catch there were over 15 years of age. Off western Nova Scotia most were under 15 years of age. As noted

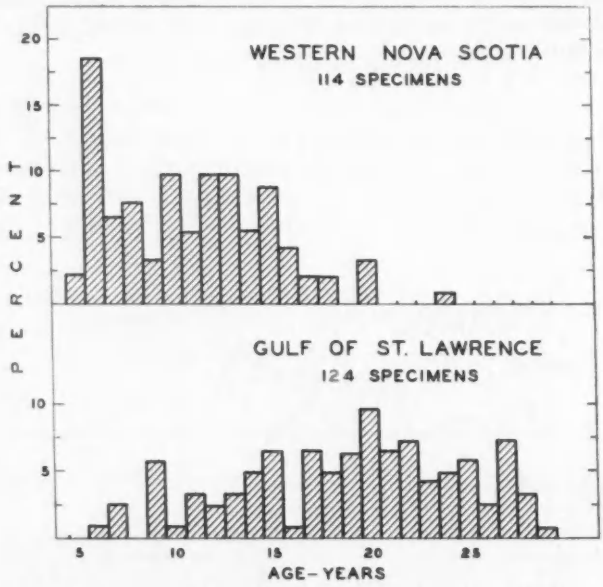

Fig. 10. Age composition of halibut in experimental catches from the Gulf of St. Lawrence (1946) and western Nova Scotia (1947).

previously, various difficulties were encountered in reading ages of the old fish. However, the difference in age composition for halibut of the two regions is greater than can be attributed to error in age determination.

Increased sampling from shallow water off Anticosti Island would undoubtedly have increased the number of young fish in the catch. Off western Nova Scotia halibut from all depths at which they were available were sampled for age. The relative absence of old fish, therefore, seems real.

Comparison of Growth Rates

Male and female. In both the southern and northern regions female halibut were found to grow larger than males. The difference is particularly apparent

for the growth in weight (Fig. 11). Up to 9 or 10 years the difference in size between males and females of the same age is not marked. Beyond this age, however, females grow at a faster rate than do males. At 9 years of age males averaged about 16 lb. (ca. 87 cm.), females about 20 lb. (ca. 91 cm.). At 15 years of age males averaged about 45 lb. (ca. 120 cm.), females about 80 lb. (ca. 140 cm.).

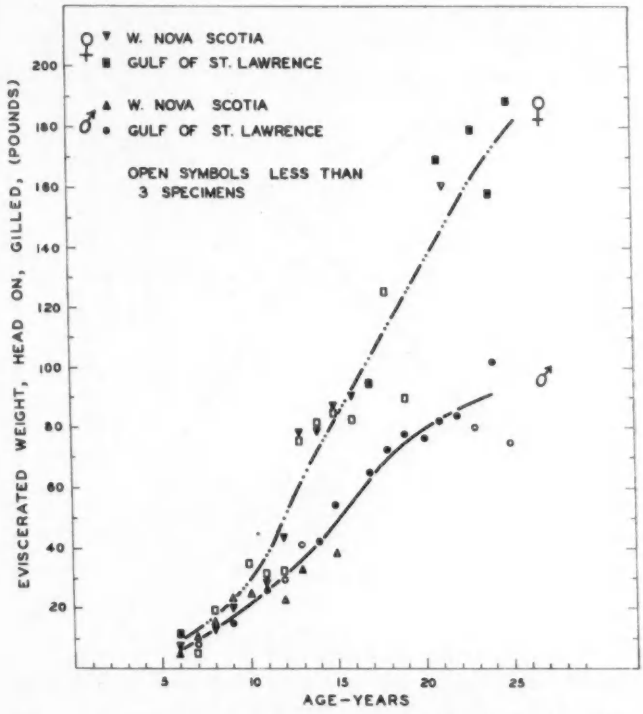

FIG. 11. Comparison of growth in weight of male and female halibut.

While the number of age estimations made is relatively small, the difference between males and females is so marked that there can be little doubt that it is real. Jespersen (1917) has shown a similar difference in growth rate between males and females off Iceland; Thompson (1914) reports it for the Pacific halibut; and it is known in many other flatfishes.

GULF OF ST. LAWRENCE AND WESTERN NOVA SCOTIA. Male halibut off western Nova Scotia are slightly larger than those off Anticosti Island at the same age, during their earlier years (Fig. 12). However, it appears that the growth rate of male halibut off western Nova Scotia slows down at an earlier age than that off Anticosti Island. Thus, at ages over about 12 years, males from Anticosti Island are growing faster.

The relatively small numbers of fish, the scarcity of young fish in the Gulf of St. Lawrence samples, and the small numbers of old fish in the Nova Scotian sample, make comparison difficult. Differences in size at age between male halibut from western Nova Scotia and the Gulf of St. Lawrence are of the same order as differences between Icelandic populations (Jespersen, 1917), and less than that for some Faroese populations (Joensen, 1954).

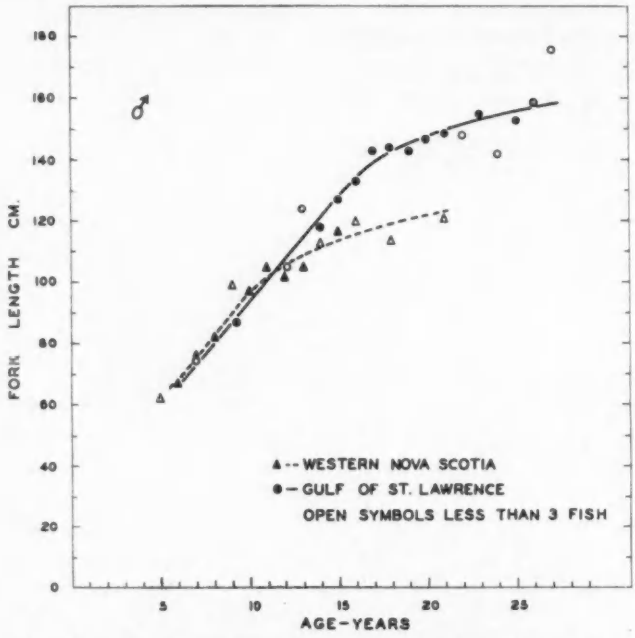

FIG. 12. Comparison of growth of male halibut from the Gulf of St. Lawrence and western Nova Scotia.

In contrast to the males the size at age of female halibut from the Gulf of St. Lawrence and western Nova Scotia is similar within the ages represented in the samples (Fig. 13). Although few females older than 16 or 17 years were caught off western Nova Scotia, they were also similar in size at a particular age to those from the Gulf of St. Lawrence.

The data suggest that male halibut from western Nova Scotia seldom reach the large size of those in the Gulf. Females may, but their numbers are much reduced. Possibly a more intensive fishery reduces the numbers of older fish, although Huntsman (1918) shows that American plaice, *Hippoglossoides platessoides*, from warmer waters seldom reach the ultimate size of those in the colder Gulf of St. Lawrence. He believes that a higher death rate in warmer areas is responsible.

SUBAREA 4 AND OTHER AREAS. Growth of Halibut in Subarea 4 is compared with that of other North Atlantic areas in Fig. 14 and 15. With the exception of northern Norway, old fish are not well represented in the comparative data. Younger male and female halibut from Subarea 4 grow more slowly than those

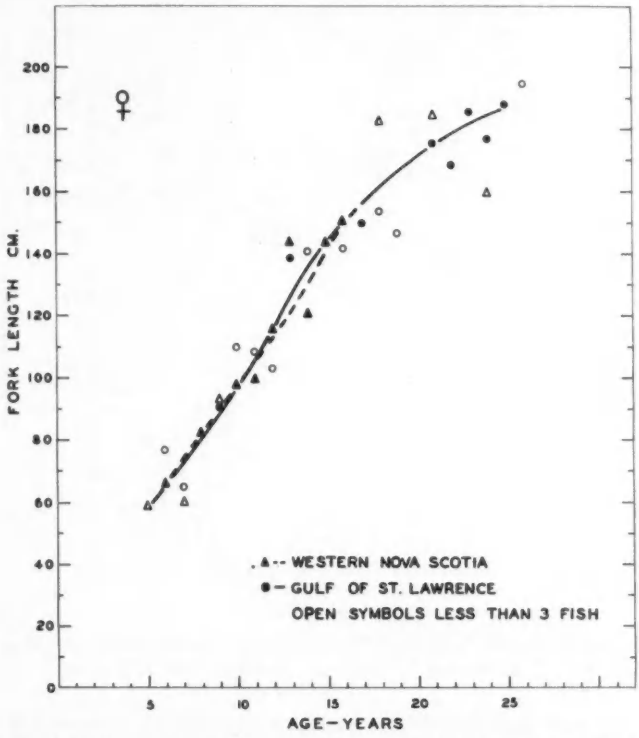

FIG. 13. Comparison of growth of female halibut from the Gulf of St. Lawrence and western Nova Scotia.

of the Faroes, and at about the same rate as those from Greenland. Older male halibut from Subarea 4 grow faster than those of north Norway, while older females from these two areas grow at similar rates.

Gear selection, interpretation of ages, etc., probably tend to bias the details of these comparisons, but it appears that growth rates for halibut in Subarea 4 are within the range found in other areas.

SPAWNING AND MATURITY

Observations on spawning season and age and size at maturity allow gross comparisons and preliminary conclusions. They are included only because such information is lacking for the halibut in the northwest Atlantic. Bigelow and

Schroeder (1953) discuss this phase of the halibut's life-history but rely chiefly on a relatively few observations from the European side of the Atlantic, and the well described life-history of the Pacific halibut.

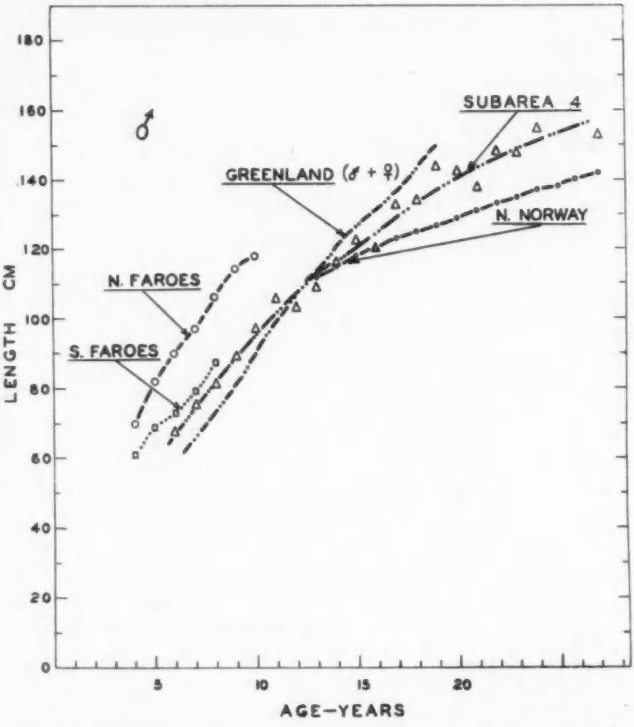

FIG. 14. Comparison of male halibut growth for different regions of the north Atlantic. Sources of growth curves are: Norway—Devold (1938); Greenland—Jespersen (1917); N. and S. Faroes—Joensen (1954).

SPAWNING SEASON. In late May, 1945, most mature male halibut caught off Anticosti Island and Bay of Islands, Newfoundland, were recently spent. All mature females were spent, probably recently spent (W. R. Martin, personal communication). In late May and June, 1946, none of the halibut tagged off Anticosti extruded milt or ova while being handled.

Condition of the gonads in mature halibut examined off Anticosti Island in 1946 and off western Nova Scotia in 1947 is summarized in Table VIII. Additional halibut were examined in September off Anticosti by a crew member of the *J. J. Cowie*. His records showed that no mature male and female halibut were spawning at that time.

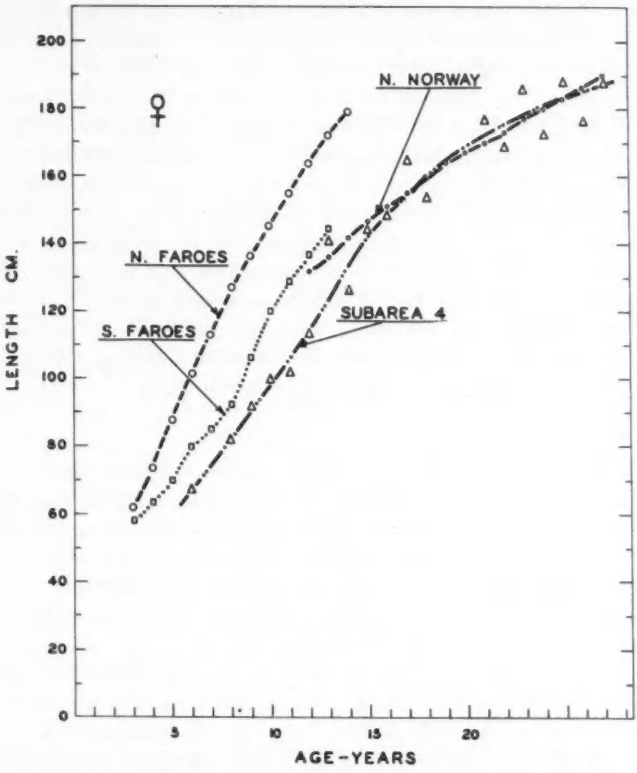

Fig. 15. Comparison of female halibut growth for different regions of the north Atlantic. (Sources same as for male halibut, Fig. 14.)

Table VIII. Condition of gonads for mature male and female halibut off Anticosti Island and western Nova Scotia.

Region	Time	Summary of observations	
		Males	Females
Gulf of St. Lawrence	May to July 1945 and 1946	23 mature males examined: 8 males extruding milt, remainder with residual milt or soft, bloodshot gonads	22 mature females examined: all judged to be spent
Western Nova Scotia	Late April and early May, 1947	1 mature male: spent	6 mature females: none ripe, 4 definitely spent
Western Nova Scotia	September and October, 1947	16 mature males: no evidence of milt, some gonads still soft and purplish	29 mature females: ova clinging to walls of ovary and to each other; centre of gonad empty but gonad relatively turgid

All the results suggest that halibut in Subarea 4 spawn in winter and early spring, probably in March or April. These results are contrary to reports, chiefly by fishermen, (McKenzie, 1946; Bigelow and Schroeder, 1953) that halibut spawn throughout the summer or in early autumn in the Subarea 4 region. However, Tåning (1936) concluded that halibut in the northeast Atlantic spawn in winter, chiefly in March, April, and May. Winter spawning is reported also for the closely-related Pacific species (Thompson and Van Cleve, 1936).

No marked spawning migration has been detected by these investigations or from a consideration of commercial fishing records. The distribution of halibut off Anticosti Island and off western Nova Scotia suggests that spawning does not take place in shallow water. The Pacific halibut is known to spawn in deep water, 150 to about 225 fathoms (Clemens and Wilby, 1946). In the northeastern Atlantic it is believed to spawn in even deeper water (Tåning, 1935). In Subarea 4 halibut probably spawn in depths of about 100 fathoms.

Size and Age at Maturity

In the Gulf of St. Lawrence mature halibut predominated in the catch (Tables IX and X), while off western Nova Scotia immature and mature fish were more nearly equal in numbers. It was relatively easy to determine by gross examination whether or not female halibut were mature. For males it was much more difficult, particularly late in the season after spawning had been over for some time. Observations of male halibut examined in September from the Gulf of St. Lawrence have been omitted for this reason.

Male halibut mature at a smaller size than females. Appreciable numbers of male fish were mature at about 80 cm. in length, while few females under 110 cm. were mature. All male halibut over 110 cm. were mature, while a few females up to 130 cm. were immature. This size difference at maturity between males and females does not necessarily mean a difference in age at maturity. It is consistent with the difference in growth rate between the two sexes.

Table IX. Size at maturity for male halibut from ICNAF Subarea 4.

Length group	Gulf of St. Lawrence		Western Nova Scotia		Total	
	Immature	Mature	Immature	Mature	Immature	Mature
cm.	*no.*	*no.*	*no.*	*no.*	%	%
40–49	...	...	2	...	100	0
50–59	...	...	3	...	100	0
60–69	...	...	8	...	100	0
70–79	1	...	11	1	92	8
80–89	2	...	7	2	82	18
90–99	2	...	6	3	73	27
100–109	...	...	1	8	11	89
110–119	1	...	...	1	50	50
120–129	...	2	...	3	0	100
130–139	...	...	...	1	0	100
140–149	...	5	...	...	0	100
150–159	...	3	...	...	0	100
160–169	...	...	...	...	...	...

Conclusions concerning age at maturity are based on observations of very few specimens. In the Gulf of St. Lawrence 10 female halibut ranging from 4 to 12 years of age were immature, while 48 females between 13 and 29 years of age were mature. However, there were only 3 fish in age group 13 and only 1 each in the age groups 10, 11, and 12. Thus, no estimate of the percentage of females maturing earlier than 13 years can be made.

TABLE X. Size at maturity for female halibut from ICNAF Subarea 4.

Length group	Gulf of St. Lawrence		Western Nova Scotia		Total	
	Immature	Mature	Immature	Mature	Immature	Mature
cm.	*no.*	*no.*	*no.*	*no.*	%	%
40–49	...	...	...	...	...	...
50–59	...	...	3	...	100	0
60–69	1	...	6	...	100	0
70–79	1	...	19	...	100	0
80–89	2	...	7	...	100	0
90–99	...	...	4	1	80	20
100–109	3	...	13	1	94	6
110–119	2	1	8	9	50	50
120–129	...	...	4	9	44	56
130–139	...	1	...	8	0	100
140–149	...	6	...	8	0	100
150–159	...	7	...	5	0	100
160–169	...	6	...	1	0	100
170–179	...	8	...	1	0	100
180–189	...	3	...	1	0	100
190–199	...	5	...	1	0	100
200–209	...	4	...	...	0	100
210–219	...	...	...	...	...	...
220–229	...	1	...	...	0	100

Of male halibut examined during May in the Gulf of St. Lawrence, 4 fish between 7 and 11 years of age were judged immature. Two halibut of 14 and 15 years of age were mature. Other older male halibut examined at this time were all mature.

For halibut off western Nova Scotia, maturity data cannot be compared directly with age determinations. Correlating size at maturity with growth rate suggests that female halibut off western Nova Scotia mature between 10 and 12 years. Male halibut possibly mature slightly younger, from 8 to 11 years.

Age at maturity for halibut in Subarea 4 agrees well with that reported for the northeast Atlantic (Jespersen, 1917) and is similar to that for halibut of Hecate Strait and Kodiak Island in the north Pacific (Thompson, 1914). Halibut in the Gulf of St. Lawrence possibly mature later than those off western Nova Scotia. This conclusion is consistent with the greater size that halibut reach in the Gulf of St. Lawrence. However, the present data are inadequate to explore this correlation further.

LENGTH–WEIGHT RELATIONSHIP

The length-weight relationship for round and eviscerated halibut from the Gulf of St. Lawrence and for eviscerated halibut from western Nova Scotia is

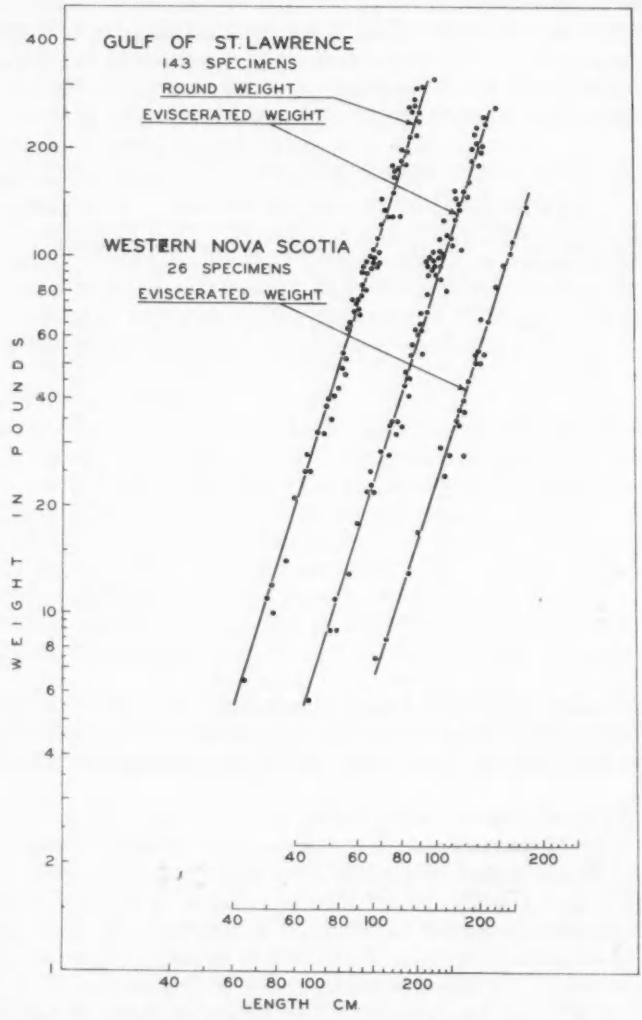

FIG. 16. Comparison of length-weight relationship for whole and eviscerated halibut from the Gulf of St. Lawrence (1946) and eviscerated halibut from western Nova Scotia (1946). (Note that logarithmic scales are used for both length and weight and that the length scales for the different categories are offset in order to show the individual lines.)

shown in Fig. 16. For halibut from the Gulf of St. Lawrence this relationship for round weight is described by the equation

$$\log y = \bar{5}.12 + 3.28 \log x$$

Here y is the weight in pounds and x the fork length. The length–weight relationship for eviscerated halibut from the Gulf of St. Lawrence is described by the equation

$$\log y = \bar{4}.99 + 3.19 \log x$$

The slopes of the two lines tested are not significantly different. Their intercepts are well separated however, and a conversion factor of 1.19 is necessary to change eviscerated weight to round weight.

For western Nova Scotia the length–weight relationship of eviscerated fish is described by the equation

$$\log y = \bar{4}.93 + 3.15 \log x$$

The difference between the slope of this line and that for halibut from the Gulf of St. Lawrence is not statistically significant. The results are useful in determining average weights for various sizes of eviscerated and round fish, but do not indicate differences between the halibut stocks in the two regions.

Other Comparisons

Dorsal and anal fin ray counts, relative head lengths, and relative lengths of pectoral fins, when compared statistically failed to show significant differences between Gulf of St. Lawrence and western Nova Scotia halibut. Differences in colour of the under surface of the halibut have been noted. Smaller halibut in both regions tended to be uniformly white on the under side. The under side of large halibut from the Gulf of St. Lawrence were usually mottled with grey. Those caught off western Nova Scotia seldom showed this mottling. Often, however, western Nova Scotia fish had a pronounced reddish tinge on the under side. These are known to fishermen as "cherry-bellies". This condition was not observed in the Gulf of St. Lawrence.

While meristic characters and proportional growth characteristics fail to show statistically significant differences between the stocks, the evidence from recaptures of tagged fish, age and size composition, and growth rates support the conclusion that these halibut stocks are discrete.

THE HALIBUT FISHERY IN SUBAREAS 3 AND 4

Landings, 1920 to 1955

Annual landings of halibut from Subareas 3 and 4 have averaged about 5 million pounds since 1920, with relatively wide fluctuations in some periods (Fig. 17). From 1920 to 1940 landings were relatively stable and close to the long-term average. Landings decreased in 1940, remained low through 1948, and then increased sharply to about 13 million pounds in 1950. In 1952 landings declined and since that time have remained near the long-term average.

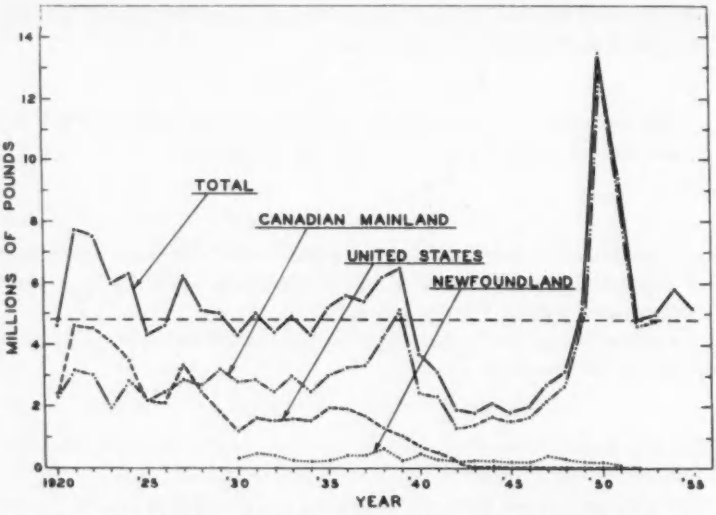

FIG. 17. Halibut landings from Subareas 3 and 4, eviscerated weight, head on.

From 1920 to the late 1930's United States linefishing vessels landed about one-half of the halibut caught in Subareas 3 and 4 (Fig. 17), but since about 1938 the Canadian fleet has landed practically all the halibut taken. Most of these were caught by vessels landing at Canadian mainland ports. Newfoundland landings have been low. Fluctuations in landings during the past 15 or 20 years have been related mainly to changes in effort by the Canadian fleet.

THE CANADIAN FISHERY

Canadian mainland halibut landings can be divided into three groups. These are: from the offshore halibut fishery by dory vessels and large longliners; from the inshore halibut fishery with small and medium longliners; and from the other offshore and inshore fisheries which take halibut incidentally while fishing for other species. Recent landings of halibut by each of these groupings of the fleet are presented in Table XI. Only the first two sources produce an important part of the total weight of halibut landed. However, the latter group may produce relatively large numbers of small fish. Conveniently, each of these fisheries can be discussed separately.

THE OFFSHORE FISHERY GROUP

Landings by offshore vessels fishing for halibut have fluctuated widely since 1940 (Fig. 18). Landings prior to 1940 are not strictly comparable since all offshore vessel landings were grouped together, and included the incidental halibut catch as well. Fluctuations in the catch and the proportions taken offshore were less marked than in recent years. Prior to 1940 the catches from offshore usually comprised over one-half of the landings of halibut.

TABLE XI. Proportion of halibut landings attributed to different fishery groups.

Year	Inshore boats	Offshore boats	Hook and line: Offshore vessels, incidental	Hook and line: Offshore vessels, halibuting	Otter trawlers, mainly offshore	Total catch
	%	%	%	%	%	*10⁶ lb.*
1947	81	19	...	13.1	5.9	2,180
1948	72.4	27.6	...	19.6	8	2,585
1949	55.8	44.2	27.8	10.4	5.9	4,800
1950	25.9	73.3	66.8	4.7	2.6	13,000
1951	23.0	77.0	70.2	4.1	2.8	8,840
1952	41.6	58.5	43.6	4.5	10.4	4,572

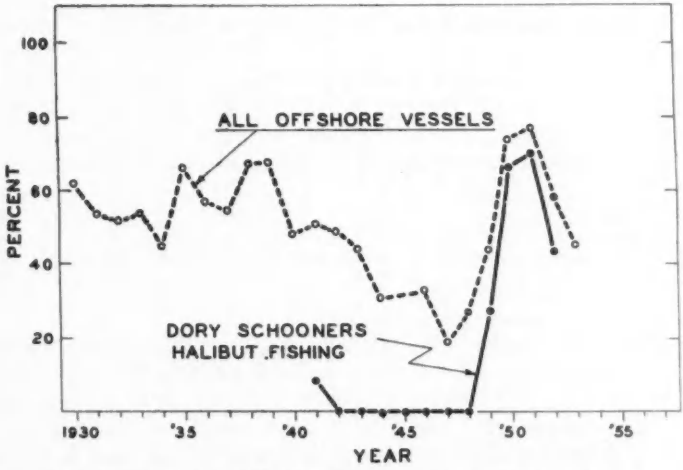

FIG. 18. Proportion of halibut landings taken by offshore vessels.

From 1942 to 1948 the offshore halibut fleet did not contribute any of the halibut landed. In contrast, they produced about 70% of the landings in 1950 and 1951, when halibut landings were at a high level. Since 1952 the landings attributed to the offshore fleet have again been about one-half of the total halibut landings (as prior to 1942).

EFFORT AND CATCH PER EFFORT. Years of peak landings appear to have been the result of increased effort by the offshore halibut fleet. McKenzie (1946) relates the higher than average landings in 1938 and 1939 to increased effort by dory vessels fishing offshore. From 1942 to 1948 no dory schooners fished for halibut (Table XII). The relatively low landings at this time were produced by the inshore fleet and from incidental catches. Post-war effort began with the small dory vessels (less than 150 gross tons) in 1949. In 1950 both small and large dory vessels fished for halibut and the number of trips reached a maximum of 189.

This was the year of peak landings. Since that time the number of halibut trips has decreased to about 45–50 annually and landings have declined to a more average level. The catch per trip for the small dory vessels was at a maximum of about 43,000 lb. in 1949 (Table XIII). It decreased each year to about 16,000 lb. in 1953. Large dory vessels, not fishing in 1949, had their highest catch per effort of about 48,000 lb. per trip in 1950. Catch per trip then declined each year to about 25,000 lb. in 1953. More recently one dory vessel using longline gear from the vessel averaged about 22,000 lb. per trip in 1955.

TABLE XII. Total landings, number of trips, and average catch per trip for offshore vessels fishing halibut in thousands of pounds.

Year	Small vessels (less than 150 gross tons)			Large vessels (150 gross tons and over)		
	Landings	No. trips	Catch per trip	Landings	No. trips	Catch per trip
	10³ lb.		*10³ lb.*	*10³ lb.*		*10³ lb.*
1941	0	0	...	166	3	55.3
1942–5	Records, while not so complete as in later years, show no specific halibut trips					
1946–8	0	0	...	0	0	...
1949	1,170	24	42.7	0	0	...
1950	4,330	121	31.4	3,293	68	48.4
1951	2,610	80	28.4	2,832	79	35.8
1952	896	44	17.9	854	34	25.1
1953	689	37	16.3	420	17	24.7

Catch per effort declined in both Subareas 3 and 4, although the years of maximum catch per trip differed. Average catch per trip by small vessels was high in Subarea 3 in 1950, while in Subarea 4 it was higher in 1949 and 1951 (Table XIII). Average catch per trip for large vessels was highest in 1950 in Subarea 3. In Subarea 4 catch per trip, while high in 1950, was not as high as that in 1951. However, both regions show the same rapid decline in catch per effort for halibut since 1951.

SIZES OF HALIBUT LANDED. No samples of halibut landed by offshore vessels have been measured. However, the commercial size categories provide some information about the sizes of halibut landed. These size categories are defined

TABLE XIII. Halibut catches per trip by area fished, for large and small vessels, in thousands of pounds.

Year	Small vessels (less than 150 gross tons)			Large vessels (150 gross tons and over)		
	Subarea 3	Subarea 4 (4V and 4W)	Mixed and unknown areas	Subarea 3	Subarea 4 (4V and 4W)	Mixed and unknown areas
	10³ lb.	*10³ lb.*	*10³ lb.*	*10³ lb.*	*10³ lb.*	*10³ lb.*
1949	39.3	40.8	47.1	0	0	0
1950	45.8	32.6	25.5	63.9	56.7	32.0
1951	21.6	42.5	29.5	34.0	60.5	33.4
1952	19.7	29.0	16.1	32.0	0	23.3
1953	16.7	10.7	22.1	29.2	25.3	20.6

TABLE XIV. Commercial size categories of halibut and their definition for Nova Scotia ports since 1946. (The variability of culls represents differences between ports and buyers rather than a systematic, long-term change.)

Trade category	Approximate weight range	Approximate length range
	lb.	*cm.*
Snapper	2.5 – 5 to 8	48– 65
Chicken	5 to 8 – 10 to 12	66– 80
Medium	10 to 12 – 85	81–150
Large	over 85	over 150

in Table XIV. Although the limits of these size categories may vary from time to time, in general they provide an estimate of small, medium and large fish landed.

Landings of the offshore vessel fishery for halibut include mainly large and medium sizes of halibut (Table XV). In 1950, the year of peak landings, about 95% of the halibut landed by this section of the fleet were of large and medium sizes. Over half of these were in the large category. In 1952, when the landings had returned to near average levels, about 98% of the landings were of large and medium fish. However, medium fish were slightly more important than large in the total.

TABLE XV. Sizes of halibut landed from the offshore halibut fishery in 1950 and 1952.[a]

Size category	Year, weight and percentage of total			
	1950		1952	
	10^3 lb.	%	*10^3 lb.*	%
Snapper	55	0.9	5	0.3
Chicken	241	3.7	19	1.2
Medium	2,784	43.2	842	51.2
Large	3,370	52.2	778	47.3

[a]Compiled from individual landing records for the offshore fleet.

The changes in proportion of large and medium halibut landed are difficult to interpret since male and female halibut differ so markedly in size.

Only minor quantities of small halibut were landed. The scarcity of small halibut in the landings is consistent with probable selection by the large hooks used, and the relatively few small halibut found in deep water.

THE INSHORE FISHERY

Landings of halibut by inshore boats have been relatively stable compared to offshore landings. They have averaged about one million pounds per year from 1920–1948 (Fig. 19). From 1949 to 1951 landings by the inshore fleet were much higher than the average, but since that time, they have decreased to about average levels. The increased inshore landings for the years 1949–1951 are probably only partly correct since differences in allocation between Fishery Officers' reports and

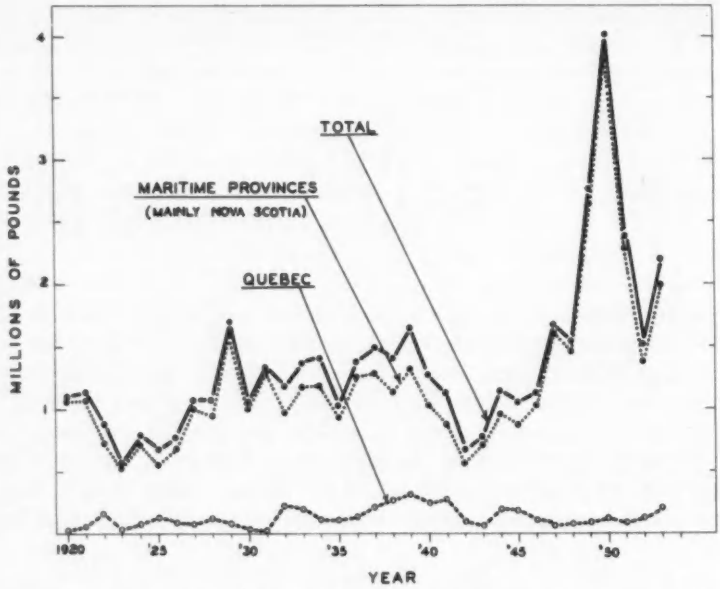

FIG. 19. Canadian inshore halibut landings (excluding Newfoundland) eviscerated weight, head on.

published statistics are known to exist. It seems unlikely that inshore halibut landings were more than about 2.5 million pounds in 1950, rather than about 4 million pounds as shown in the published statistics. Even with this reduced total, the landings in 1950 were very high and suggest increased stocks of halibut along with increased effort.

EFFORT AND CATCH PER EFFORT. As previously described, the inshore halibut fleet consists of many small and medium longliners. Estimates of their numbers are lacking. They land at a number of ports, particularly in western Nova Scotia. Some of the medium longliners fish well offshore in summer months, while most of the small longliners fish on relatively inshore grounds. It is impossible with the available statistics to separate the total catch of halibut made by those longliners fishing for halibut from the incidental inshore catch. However, catch and effort statistics are available for a small sample of the fleet. These boats began fishing halibut during the summer months in 1948 and have continued to the present. Catch per effort in Subdivision 4X reached a maximum in 1951 at about 17 lb. per line (Table XVI). Between 1948 and 1950 catch per line ranged from about 7 to 10 lb. Since 1951 catch per line decreased to about 8 to 9 lb. Catch per line in Subdivision 4W followed the same pattern. Larger boats and increased navigational and sounding equipment probably contributed to the increase in catch per line up to 1951. It seems probable, however, that part of the increase is related

to size of stock. Increased catch per unit effort in 1950 and 1951 would contribute to the increase in inshore landings. The subsequent decrease in catch per unit effort appears to represent decreased size of stock.

TABLE XVI. Catch in thousands of pounds and catch per effort (C/line) in pounds for longliners halibut fishing.

	Area 4X		Area 4W	
Year	Catch	C/line	Catch	C/line
	10³ lb.	*lb.*	*10³ lb.*	*lb.*
1948	14.4	6.7	8.4	7.2
1949	59.8	6.6	13.9	6.0
1950	45.2	10.2	85.3	8.4
1951	149.6	17.5	49.2	10.5
1952		Not available		
1953	61.3	12.7	28.0	8.4
1954	56.2	8.3	30.7	7.9

In the seasonal inshore halibut fishery off Cape Sable Island, catch per line for a sample of the commercial fleet in 1947 was about 7.5 lb. Information for other years is not available for comparison, but landings have ranged from about ¾ million pounds to about 1½ million pounds during the period 1947–1954. The years 1947 and 1948 were poor years. Landings were high in 1949 and 1950 and again in 1953 and 1954. Probably in years with good landings, catch per effort was higher than in 1947 and 1948. Changes in landings are probably related more to changes in catch per effort of halibut than to change in effort.

SIZES OF HALIBUT LANDED. Landings of the inshore halibut fleet according to commercial size categories are not available. Exploratory fishing off western Nova Scotia in 1947 caught mainly medium halibut (10–85 lb., 80–150 cm.). Measurements of halibut made from a commercial landing in 1950 gave the same information; most of the halibut were medium fish between 100–150 cm.

Measurements of halibut from the Cape Sable Island commercial fishery in 1947 and 1950 show that few small halibut were landed (Table XVII). Most fish were of medium size, generally over 100 cm. in length. The proportion of large fish, those over 150 cm., had apparently decreased between 1947 and 1950. That the inshore halibut fishery landed mainly medium and large fish is consistent with the probable selectivity of the gear used and with the distribution of large and small halibut off western Nova Scotia where this fishery is concentrated.

TABLE XVII. Sizes of halibut landed by the commercial fishery off Cape Sable Island in 1947 and 1950.

Commercial category	Length group	1947	1950
	cm.	*no.*	*no.*
Snapper	48–65	14	0
Chicken	66–80	57	3
Medium	81–150	242	144
Large	over 150	114	19

INCIDENTAL LANDINGS

Incidental landings of halibut are made from the groundfish fishing fleet while they are fishing for other species (Table XI). The vessels include both hook and line fishing vessels and all sizes of otter trawlers. Separation of the component parts of the inshore halibut landings is, however, impossible with present statistics. It is estimated that about two-thirds of the inshore landings come from the halibut fishery; the balance is produced by incidental catches.

Because individual trip statistics are collected for offshore vessels, the incidental halibut catch by vessels fishing offshore can be obtained. The incidental offshore landings are usually less than about 15% of the total weight (Table XI). The proportion of the incidental catch taken by otter trawlers has been increasing, while that taken by hook and line vessels has been decreasing. However, the total annual incidental landings during the period 1947–1952 have remained at about the same level.

EFFORT AND CATCH PER EFFORT. Fishing effort which produced the incidental catch of halibut was directed at other species. In general, the otter trawler fleet has increased in the post-war period. The dory vessel fleet has declined. These factors are consistent with the increased proportion of the incidental halibut landings taken by otter trawlers.

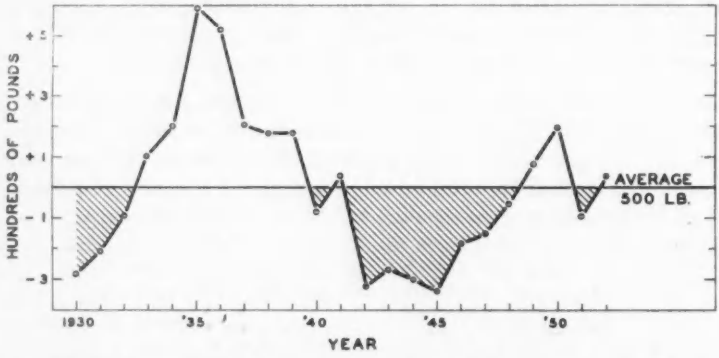

FIG. 20. Variations in halibut landings per trip for large and medium otter trawlers, 1930–1952.

Since 1947 the incidental halibut landings per trip for dory vessels has averaged slightly less than 1,000 lb. In 1949 and 1950 it was at a maximum of about 1,500 lb.

Individual trip records for otter trawlers go back to 1930. Their annual average landings of halibut per trip show fluctuations (Fig. 20). Over the period 1930–1952 they have averaged about 500 lb. per trip. Landings per trip in the

period 1933–1939 averaged about 800 lb. and in 1949–1950, 650 lb. Landings in the early 1930's and from about 1940 to 1948 as well, averaged about 300 lb. Presumably, these changes in landings should reflect the abundance of halibut in the areas fished for other species. This would be mainly on the top and along the edges of the banks at depths around 50 fathoms. However, caution must be used in interpreting these fluctuations as reflecting changes in numbers of halibut. Prior to 1945, only a few otter trawlers were operating. Fishing grounds have changed and species fished for have also varied. Variable amounts of the small-sized halibut characterizing such trips may have also been retained by the crews for their personal use. This would probably vary with the halibut/cod price ratio. All these factors may have affected the recorded catch per trip of halibut by otter trawlers.

SIZES LANDED. Incidental catches of halibut by the inshore fishery are not recorded in the statistics by size categories. Measurement of halibut from these landings has not been carried out. Observations at Lockeport of halibut landed by cod and haddock gear (6/0 Pfleuger or 16 and 17 Mustad hooks) suggest that most of these were small halibut (personal communication, D. N. Fitzgerald).

Incidental offshore halibut catches have a high proportion of small fish. For example, in 1951 about 40% of the incidental halibut landings by weight were snappers and chickens (under 12 lb.). In contrast, vessels fishing for halibut landed less than 1% by weight of these smaller fish. Both inshore and offshore incidental halibut landings have a high proportion of small halibut. Probably the smaller size hooks tend to select smaller halibut and otter trawls retain small fish. From the distribution of halibut it appears that fisheries for other species are being carried on where small halibut are most available. Both factors would contribute to the high proportion of small halibut in the incidental landings.

RECAPITULATION

Halibut landings from Subareas 3 and 4 are mainly produced by a Canadian hook and line fishery. Otter trawlers contribute little to the weight of halibut landed. The halibut fleet consisting of dory vessels and longliners has varied markedly in size during recent years. Generally, the dory vessel fishery has declined, while small, medium, and large longliners have increased. Marked fluctuations in halibut landings are correlated with the fishing effort by the offshore fleet.

From 1940 to 1948 offshore halibut fishing was not carried on. Landings depended during this time on the inshore fleet. Sharply increased effort in 1949 and 1950 produced very large landings. Catch per effort was also high at this time. Since that time, decreased catch per effort and decreased effort have resulted in more nearly average landings.

Halibut fishing vessels land mainly large and medium sizes of fish. The incidental landings are mainly small fish. This distribution of sizes in the landings is consistent with the sizes of gear used and the areas fished.

DISCUSSION

Distribution of Halibut and the Fishery

The distribution of halibut in Subareas 3 and 4 has had a major effect on the type of fishery which has developed. Results of investigations suggest relatively local stocks without extensive, regular migrations. In Subdivisions 4W, 4V, 3P and 3O, the chief halibut grounds are found along the edge of the continental shelf. These are well offshore, more than 100 miles, and only by using large, seaworthy vessels can they be fished year round. Smaller vessels do not fish the most distant of these even in summer. As a result, halibut catches must be large and availability good to attract large vessels into the fishery.

Western Nova Scotia is the only region where there has been a sustained halibut fishery by small and medium longliners. In this region where the continental shelf is closer to shore, between 60 and 100 miles, small longliners can fish the deep-water edge in good weather months. In addition, halibut are available on top of the continental shelf where small boats exploit concentrations of halibut off Cape Sable Island in late summer and autumn. For these boats smaller catches and lower availability still provide economical operations which supplement other fishing activities.

Presumably the distribution of halibut is related to temperature. Thompson and Van Cleve (1936) have described the halibut as a boreal species with important fishing grounds at temperatures between 3°C. and 8°C. The distribution of commercial sizes of halibut off Nova Scotia fits this description. Off western Nova Scotia bottom temperatures, except on top of the banks, are usually above 4° or 5°C. (McLellan, 1954). To the eastward where halibut are not taken on top of the continental shelf, temperatures are usually less than 3°C. (McLellan, 1954). At the edge of the shelf temperatures in deep water are more stable and usually above 5° or 6°C. Important halibut fishing grounds are found there and halibut apparently remain in this deeper, warmer water throughout the year.

Fluctuations in Landings

It is readily apparent that low catches during the period 1940 to 1948 are the result of lack of effort by the offshore fleet. The very great increase in halibut landings in 1950 and 1951 can be related directly to increased effort by the offshore fleet. The catch per effort of halibut in these years was also high and contributed both to the build-up of effort and the large landings. Yet, it is difficult to assign any one factor as the controlling feature in these marked changes. A number of factors are important enough to warrant consideration.

CATCH PER EFFORT OF HALIBUT. The catch per trip of halibut in deep water was high during years of peak landings in relation to more recent years. The reduced effort of the period 1940 to 1948 probably resulted in an accumulated stock of old, large halibut. These provided the basis for the high catch per trip in 1949 to 1951.

While this explanation seems most logical and is sufficient in itself, the possibility of increased recruitment cannot be overlooked. McIntyre (1956) suggests

that temporarily increased post-war catches of halibut off the Faroe Islands resulted both from the war-time rest and from good broods of halibut. Our records are insufficient to follow through this line of reasoning. However, otter trawl catches of halibut inside the edge of the banks were high in the 1930's. These fish were presumably mostly snappers and chickens, as they are at the present time. At that time they would be about 4 to 6 years old. The fish taken by hook and line vessels in 1949 to 1951 could have come from these possibly abundant broods.

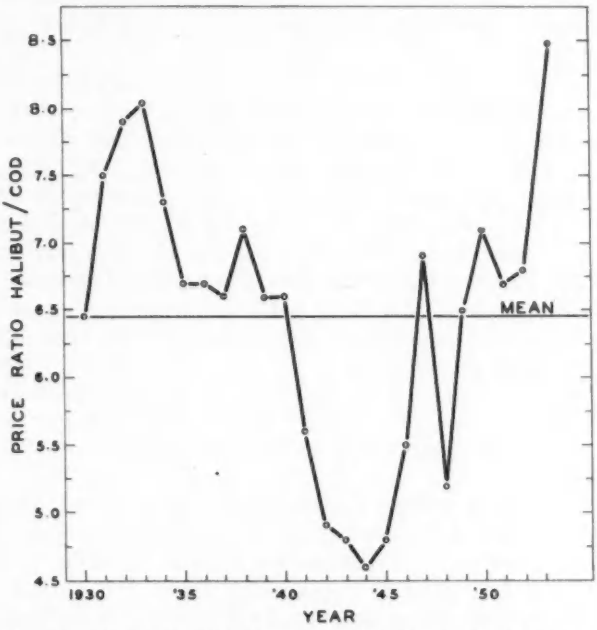

FIG. 21. Price ratio of halibut and cod landed on the Canadian Atlantic mainland.

Large catches and high catch per effort from Subdivision 4X in 1950 and 1951 support the view that recruitment from several good year-classes contributed to the high landings in 1950 and 1951.

LANDINGS OF OTHER SPECIES AND ECONOMIC FACTORS. Low halibut landings and reduced halibut fishing effort from 1940 to 1948 occurred during a period of high cod landings which reached a peak in 1946 (Martin and McCracken, 1952). Cod were abundant and both dory vessels and otter trawlers made large landings of this species. As a result, an unknown stock of halibut offered little attraction. In addition, the average halibut:cod price ratio was much below average (Fig. 21), and fishing for halibut offered comparatively low rewards. Also, halibut fishing gear was difficult to obtain and expensive.

Decreasing catch per effort of cod, an increased halibut:cod price ratio and high catch per effort of halibut all contributed to the increased effort for halibut in 1950 and 1951. The halibut:cod price ratio remained high in 1952 and 1953, and the catch per effort of cod remained at a relatively low level. The decreased effort for halibut in these years seems directly related to the lowered availability of halibut. The deciding factor was probably economic returns.

RATIONAL UTILIZATION OF SMALL FISH. Present data are inadequate to reach concrete conclusions concerning the advantages of saving small fish for later capture. However, they do provide suggestions that such action might increase the sustained yield of halibut.

It is known that small halibut from 3 to 10 pounds are found on top of the banks and are vulnerable to capture by gear fishing for other species. Halibut smaller than this have not generally been recorded. Descriptions of halibut distribution in other regions generally suggest that very young halibut are found in shallow, coastal bays around Iceland, the Faroes, and on the Pacific Coast (Joensen, 1954; McIntyre, 1956; Thompson, 1915). Extensive dragging with small-mesh gear along the Canadian mainland did not catch small halibut. One specimen, 18 cm. long, was captured in the shallow water of Passamaquoddy Bay, N.B., in 1948. It is believed that in the Subarea 4 region halibut probably settle and remain on the shallow parts of offshore banks. Large quantities of small halibut (5 specimens ranged from 29–34 cm.) were taken by otter trawl in December, 1946, at depths of 28 to 30 fathoms on Sable Island Bank. However, it is claimed that it is unusual to capture halibut of this size in quantities. Presumably, these youngest, fastest growing fish are usually protected from exploitation by their distribution.

Those taken by otter trawlers and small hooks are fast growing fish (Fig. 22). Snapper halibut, under about 5 to 6 pounds, are increasing in weight about 70% per year. Chicken halibut, 5 to 10 pounds, are probably increasing in weight about 40% per year. It seems likely that loss in weight to the halibut stock by natural mortality of the small fish would only be a small fraction of their gain by growth.

Complicated fishing conditions tend to make the problem difficult to assess. By weight, the landings of small halibut from offshore banks are unimportant. However, estimates of their numbers suggest that they may equal or exceed the

TABLE XVIII. Weight of halibut landed from offshore banks and estimates of their numbers by size categories. Average sizes used to estimate numbers are: large—100 lb., medium—50 lb., chicken—10 lb., and snapper—5 lb.

Year	Weights of halibut landed				Numbers of halibut landed					Percentage chicken and snapper
	Large	Medium	Chicken	Snapper	Large	Medium	Chicken	Snapper	Total	
	10^3 lb.	*10^3 lb.*	*10^3 lb.*	*10^3 lb.*	*10^3 fish*	*10^3 fish*	*10^3 fish*	*10^3 fish*	*10^3 fish*	%
1949	445	1,293	212	170	4	26	21	34	85	65
1950	4,530	4,332	480	288	45	87	48	58	238	45
1951	3,680	2,800	200	135	37	56	20	27	130	36
1952	1,040	1,310	175	147	10	26	18	29	83	57
1953	595	1,049	168	212	6	21	17	42	86	68

numbers of medium and large halibut landed (Table XVIII). It is believed that estimates of small halibut may be low, since crew members often take home small halibut which would not be included in the landings. While these estimates are crude, they do point out that a large number of small, fast growing fish are being taken.

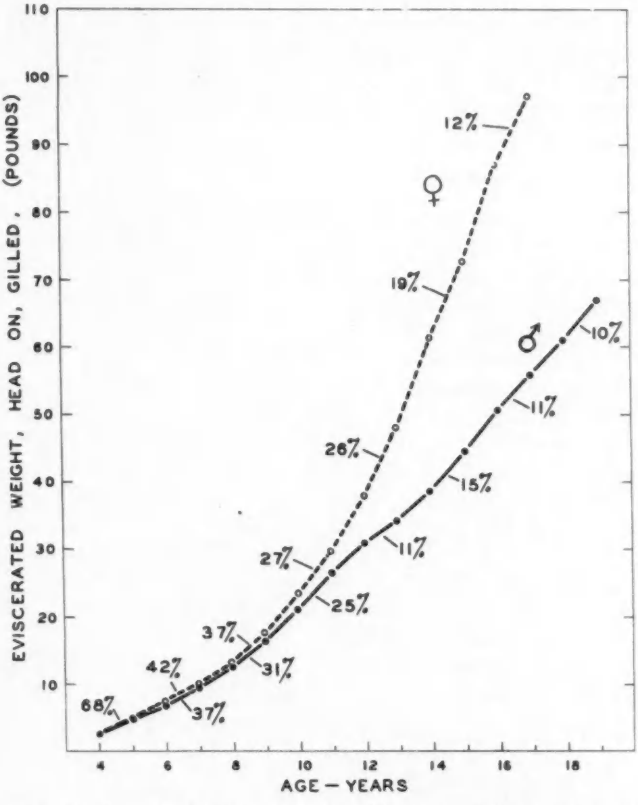

FIG. 22. Rate of weight increase for halibut from Subarea 4. Average values for halibut from all regions and sources, including some obtained from otter trawl catches of small fish.

From these estimates it seems that the problem warrants much more detailed investigation. Such investigation would involve measurements and age determinations from commercial landings of all sections of the fishery. However, particular emphasis should be placed on the offshore catches, both taken incidentally or as the primary object of a fishery.

Even with the limited data available, it seems logical to expect that increasing the age at first capture for halibut would increase the sustained yield. The local nature of the stocks suggest that halibut released would benefit each local area. Since most of the small halibut landed are taken by gear used to catch other species, any attempts to regulate the catching of small halibut would be difficult. To design gears which would take other groundfish and not small halibut is probably impossible. Returning small halibut to the water after they have been taken on the deck of the vessel seems an obvious solution. Bell (1956) suggests that a high percentage of these would be alive. Such action would be extremely difficult to regulate. In addition, the fishermen taking most of the small halibut would probably not gain directly. Incentive for voluntary saving of small halibut is thus lacking.

Prediction of Future Yields

The only basis for estimating the future yield of halibut from Subareas 3 and 4 is the long-term statistics of the past fishery. These statistics suggest that future average annual yield should be about 5 million pounds per year. Various factors such as hydrographic conditions or changes in fishing methods might affect the long-term yield. Ketchen (1956) suggests that long-term fluctuations in the abundance of the Pacific halibut may be related to changes in water temperatures. For the Canadian Atlantic Coast, major temperature fluctuations (Hachey and McLellan, 1948) have not produced effects which can be separated from that of the fishery. It seems likely that changes in fishing levels might have more effect than hydrographic changes. In comparison with cod and haddock, for example, the size of the stocks of halibut is small. Intensive fishing for halibut would probably have rapid and major effects. The rapid decrease in availability of halibut in Subareas 3 and 4 following increased effort in 1950 and 1951 suggests that stocks can be reduced rapidly by increased fishing. Halibut may be particularly vulnerable to high fishing intensities as has been suggested for other regions (Devold, 1938; Thompson *et al.*, 1931).

Since hook and line methods appear to be the most effective method of catching halibut in Subareas 3 and 4, Canadian fishermen will probably continue to take the bulk of the landings. The development and expansion of the medium longliner fleet will probably tend to decrease the range of annual fluctuations in halibut landings which has occurred in the past.

SUMMARY

1. Halibut were studied in the northern Gulf of St. Lawrence in 1945 and 1946 and off western Nova Scotia in 1947. Statistics of commercial halibut fisheries since 1920 have also been analysed.

2. What appear to be local stocks of halibut are available in deep water from May to September off Anticosti Island. They are least available in deep water in mid summer during the time a shallow-water commercial fishery is being carried

on. This fishery takes mainly small halibut and large female halibut, which presumably have moved into shallow water as the bottom water warms there. Large male fish predominate in the catches from deep water in mid summer.

3. Recaptures of tagged halibut off western Nova Scotia suggest that halibut stocks of the LaHave–Roseway–Baccaro Banks region intermingle but mix little with stocks to the westward in the Browns–German Banks–Cape Sable region.

4. Seasonal movements between deep and shallow water are not shown by the tagging results. Halibut exploited off Cape Sable Island in late summer probably come from about the same depths around German and Browns Banks.

5. Size and sex composition of the halibut catches differed with depth. In small samples from deep water at the edge of the continental shelf most of the catch was large male fish and small fish of either sex were not taken. In shallower water, under 60 fathoms, small fish were more abundant and females predominated in the catches of large fish.

6. Best catches were made in water of intermediate temperatures, between about 3° to 5°C. in the Gulf of St. Lawrence, and between 4° and 8°C. off western Nova Scotia. None were caught at bottom temperatures less than 2.5°C., and their movements into the shallow water off Anticosti Island and to the inshore grounds off Cape Sable Island occurred as bottom temperatures warmed there to 7° or 8°C.

7. Older, larger male and female halibut were taken in the Gulf of St. Lawrence than off western Nova Scotia. In both regions, females grew faster than males, particularly after 8 to 9 years of age, and reached a much larger size.

8. Faster-growing male halibut from western Nova Scotia did not reach the same ultimate size as those from the Gulf of St. Lawrence. Growth for female halibut from the two regions showed less difference than that of males. Subarea 4 halibut grow more slowly than those of the Faroes, possibly slightly faster than those off north Norway, and about the same as halibut off Greenland.

9. Halibut in Subarea 4 probably mature at about 10 to 14 years of age and spawn in deep water in the late winter and early spring.

10. Halibut stocks from the Gulf of St. Lawrence and western Nova Scotia did not differ significantly in length-weight relationship, anal and dorsal fin ray counts, or relative body proportions. Differences in age and size composition, growth, and the results of tagging suggest that they are probably separate stocks.

11. Long-term average annual landings of about 5 million pounds of halibut from Subareas 3 and 4 have fluctuated markedly in recent years. Much below average landings from 1940–48 increased sharply to an all time high of about 13 million pounds in 1950. More recent landings have been close to the long-term average.

12. Since the late 1930's the Canadian mainland fleet has caught almost all the halibut taken from Subareas 3 and 4. Recent fluctuations have been directly related to the efforts of a large-vessel fleet fishing for halibut. Low effort from 1940 to 1949 probably resulted in an accumulated stock of halibut which was fished heavily in 1950 and 1951 due to various economic factors.

13. Vessels fishing offshore for halibut use large hooks, fish deep water and catch mainly large, mature fish. Vessels fishing for cod and haddock with smaller gear take many small, fast-growing halibut from shallower water. By weight, incidental landings contribute little, but the numbers of halibut landed may exceed the numbers landed from the halibut fishery. It seems probable that increased yield of halibut could result from saving these smaller, faster-growing fish. Even though releasing small halibut would involve much practical difficulty, the problem needs further study.

14. Long-term historical landing statistics suggest that halibut yield from Subareas 3 and 4 will continue at about 5 million pounds annually unless fishing intensity changes markedly. It is expected that Canadian hook and line fishermen will continue to take most of these landings.

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This study was carried out under the direction of Dr. W. R. Martin and I wish to express my appreciation for his advice and encouragement. I am indebted to Dr. A. G. Huntsman of the University of Toronto for many helpful suggestions during preparation of the M.A. thesis, from which parts of this paper are derived. Dr. R. Kempton, acting as observer on the *J. J. Cowie* during the summer of 1947, collected most of the exploratory fishing data off western Nova Scotia for that year. I would like also to express my appreciation for assistance given by various staff members of the St. Andrews Biological Station.

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Age and Growth of Smelt, *Osmerus mordax* (Mitchill), of the Miramichi River, New Brunswick[1]

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ABSTRACT

Smelt develop scales at 20 to 25 mm. length. The circuli or ridges on them grow from the anterior and posterior to meet laterally. The posterior free part of the smelt scale is larger than the anterior and is used in age determinations. When scale growth ceases during winter a "scar" or "line" forms just outside the incomplete ridges around the edge of the scale. Hatching occurs in early summer. Scales generally develop 2 to 3 months later. Some scales are only clear platelets at the end of the first growing season. The "line" which forms around the margin of each scale is the only evidence of the first annual growth check. A positive correlation exists between number of ridges formed on the scales during the first year and lengths of fish within a year-class. There is no significant difference in weight of the sexes at the same length during the fishery, though females do have a faster growth rate than males, accelerating as they grow older. In the fishery and at spawning the average size of different ages declines as the season progresses. Smelt in the Miramichi generally mature at the end of their second year when 105 to 120 mm. long. They are caught in the commercial fishery in quantity for the first time during the winter preceding the end of their second year when they usually comprise about two thirds of the catch. Early hatching is correlated with greater growth in the first year and this greater size persists as smelt grow older.

INTRODUCTION

The annual Canadian smelt catch is about 7 to 8 million pounds with a landed value of 1¼ million dollars. About a third of this production is from the area of the Miramichi River in northeastern New Brunswick. A decline in landings from the Miramichi over a 25-year period caused increasing concern for survival of the fishery and resulted in the Fisheries Research Board of Canada starting an investigation in 1941.

To assess the contribution of each year-class to the commercial fishery, a method of age determination was necessary. This account deals with the age and growth of smelt of the Miramichi area as determined from their scales.

METHODS

Samples of spawning-run smelt were secured from streams from late April to early June by means of dip nets or small trap nets, both made of ¾-inch (ca. 19 mm.) stretched mesh netting. This netting retained all sizes of smelt found in spawning runs. Samples from the commercial fishery were obtained from December 1 to late February, chiefly from double-end box nets (McKenzie, 1946) made of 1¼-inch (ca. 29 mm.) stretched mesh netting. This netting permitted some of the smaller fish to escape.

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Smelt from the yolk sac stage to 30 and 40 mm. long were taken in plankton nets suspended in stream currents. Larger smelt of the 0 age group were taken late in the summer and early autumn with seines (½-in., ca. 13 mm., stretched mesh) along the shore in the lower part of the Miramichi River.

The length of each fish was recorded to the nearest millimetre from tip of snout to end of scales on caudal peduncle. Standard length or length to end of vertebrae is approximately 2% less and fork length or length to fork of tail is approximately 6% greater. The weight of each fish was recorded to the nearest tenth of a gram.

All fish except those in the 0 group were measured and weighed in the fresh condition. The 0 group was preserved in 5% formalin.

Scale samples were taken from the side of the fish just posterior to the dorsal fin and were examined dry in a watch glass, or between glass slides, under low magnification. Daylight or a desk lamp provided the bright field of transmitted light used in examination.

Ages of smelt caught at spawning time are recorded as complete or full years, e.g. age 2. Fish caught during the winter commercial fishery are designated by the numerical age they would attain the next spring, this being followed by a minus sign to indicate that they had not yet completed the full period indicated, e.g. age 2–.

Tracings of scales from fish of different ages (Fig. 1–7) are arranged so that the anterior end of the scale is towards the bottom of the figure.

AGE

To interpret the structure of scales for age estimation it is necessary to understand the process of their formation and development.

Figure 1 shows the development of the smelt scale during the first summer of growth. Scales appear first as small translucent plates along the sides posterior to the dorsal fin on fish 20 to 25 mm. long. They are round or slightly elliptical and bear no markings. When the fish are 25 to 28 mm. long, ridges or circuli appear successively on the anterior end of the scale and grow posteriorly around the sides. After 3 or 4 ridges have formed anteriorly, others begin posteriorly and grow forward around the sides to meet the anterior ones. At this time the fish are 38 to 40 mm. in length. Throughout the growing season portions of ridges continue to be laid down anteriorly and posteriorly and grow toward each other to form complete ridges. In the winter, when fish and scale growth slows, many ridges are left incomplete (Fig. 2, 3). With the start of growth in the spring, new and complete ridges are formed (Fig. 4). As in many other species of fish, the bands of incomplete ridges were considered to be winter checks and by counting them the age of the fish was obtained. However, critical examination shows that each band of incomplete ridges has associated with it a bright "shiny" line or scar. This shiny line frequently occurs before any complete ridges are laid down (Fig. 2, 3, 5). The possibility may be considered that this is a winter check formed on the scales before any ridges were laid down. This interpretation would

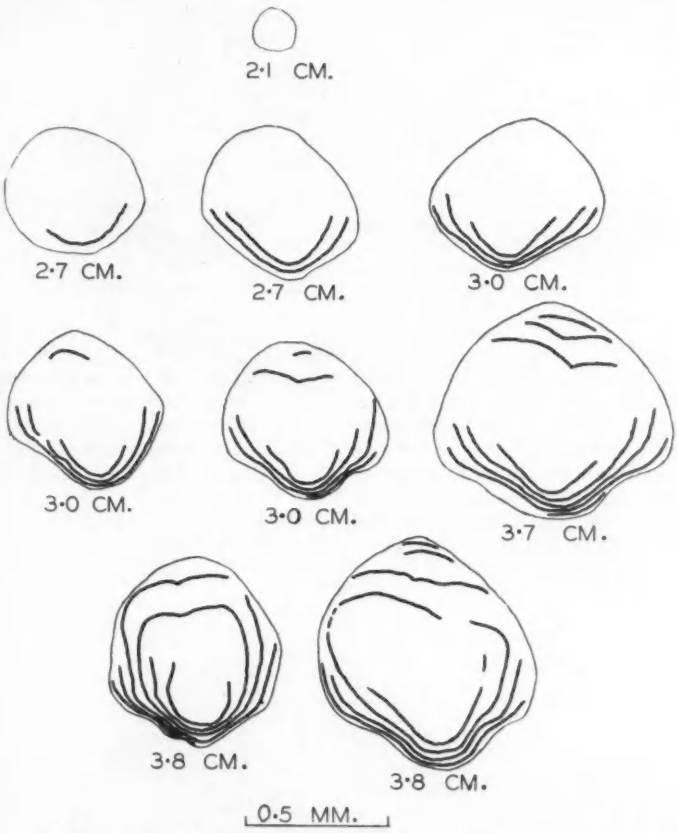

FIG. 1. Tracings of projected scales showing ridge growth in smelt of different lengths during the first summer. Anterior ends of scales are towards the lower edge of the figure.

explain why some 22% of late spawning smelt (when aged by counting bands of incomplete ridges on the scales) were assigned ages that seemed to be one year too low. These scales showed, in contrast to the majority, that the greatest number of ridges was in the first growth zone (instead of the second), and contributed to a second smaller mode in the distribution of first year ridge numbers.

Using the shiny-line criterion, a survey of the scales shows that in the first growth zone the number of ridges varies from 0 to 19 with an average of 10 or less (Fig. 4, 6, 7) in the majority of samples of over a hundred fish of all ages. In the second growth zone, the ridges vary from 10 to 20 with an average of about 15, while in the third growth zone there are from 4 to 12 with an average of 7 or 8. Subsequent growth zones have fewer ridges. This shows that the greatest

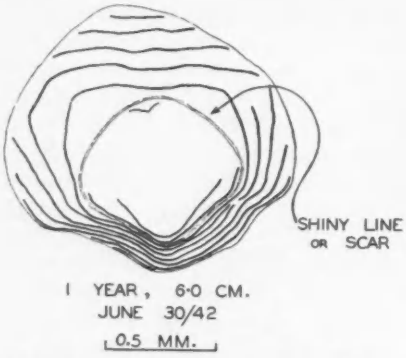

FIG. 2. Tracing of a projected scale from a 6-cm. smelt taken the end of June during its second summer. The "shiny line" on the clear central portion denotes the end of the first season's growth and the incomplete ridges at the margin were forming during the second season's growth. Anterior end of the scale is towards the lower edge of the figure.

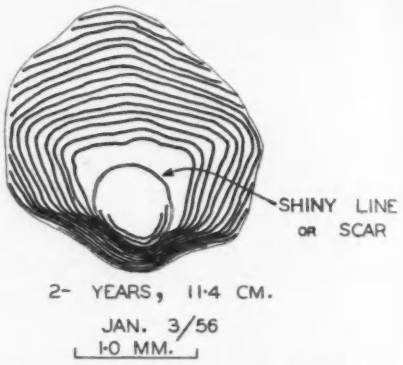

FIG. 3. Tracing of a projected scale from a smelt 2- years of age with no posterior ridges in the first season's growth inside the first "shiny line". Anterior end of the scale is towards the lower edge of the figure.

FIG. 4. Tracing of a projected scale from a smelt 2- years of age with many ridges in the first season's growth inside the first "shiny line". Anterior end of the scale is towards the lower edge of the figure.

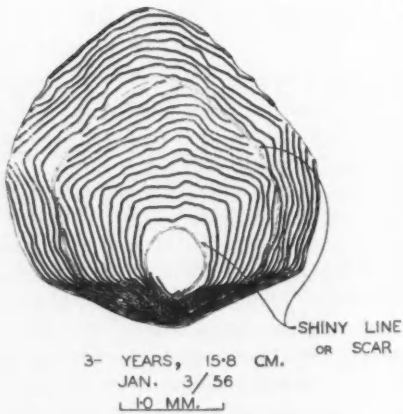

FIG. 5. Tracing of a projected scale from a smelt 3- years of age with no posterior ridges in the first season's growth inside the first "shiny line". Anterior end of the scale is towards the lower edge of the figure.

FIG. 6. Tracing of a projected scale from a smelt 3– years of age with few ridges in the first season's growth inside the first "shiny line". Anterior end of the scale is towards the lower edge of the figure.

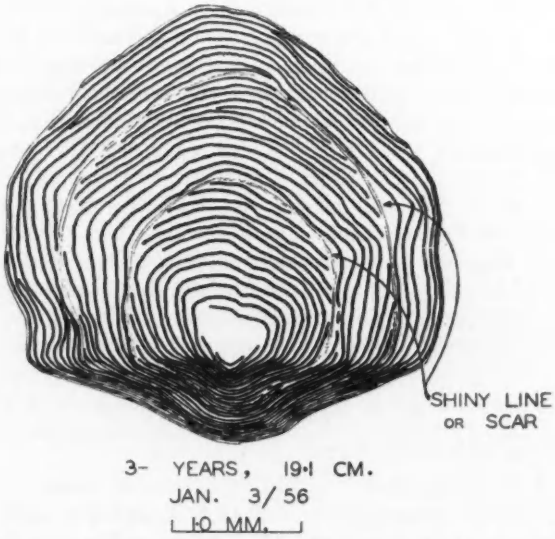

FIG. 7. Tracing of a projected scale from a smelt 3– years of age with many ridges in the first season's growth inside the first "shiny line". Anterior end of the scale is towards the lower edge of the figure.

number of complete ridges occurs in the second growth zone or during the apparent second growing season, and not in the first growth zone or during the apparent first growing season.

Evidences from water temperatures, hatching times and growing season—those factors influencing early growth and development of the fish and scale—all substantiate the shiny line as the true criterion of an annulus. They also show that the numbers of ridges in the different growth zones vary directly as the length of the growing seasons during the life of the smelt.

From mid-April to mid-December the water of the Miramichi System is not usually ice-covered as in the other 4 months of the year. During winter, water temperatures in the lower River and Bay go as low as –1.5°C., then begin to rise in early April reaching 5°C. late in April and 10°C. by the end of May. Mid-summer temperatures go as high as 25°C., usually remaining over 20°C. from early July into September. Cooling in autumn brings water temperatures down to 5°C. again during early November.

Smelt spawn from late April to early June and hatching occurs from the third week of May to late July. Smelt reach a length of 20 to 25 mm. by late July and early August, 2 to 2½ months after hatching. Smelt hatched late in the season might well have little scale growth by winter. Normally scale growth and ridge formation is confined to approximately the last half of the first growing season. During the second year, with water temperatures rising rapidly in April, body and scale growth begin much earlier than in the first year (Fig. 2). At the beginning of the third growing season the fish reach sexual maturity. Feeding and growth are not resumed until spawning is completed and the fish are back in brackish water late in May and June. Subsequent growing seasons are also shortened because of spawning every spring. The longest uninterrupted growing season for smelt thus occurs during their second year of life.

It is concluded that scales of fish which made a small first year's growth because of late hatching or for other reasons remain as small unridged plates during the first winter. The only evidence of the first winter's check in growth on the scales of these fish is the shiny line in the clear area toward the centre of the scale. When this line is counted as the first winter check, discrepancies between age and length disappear. Therefore the shiny line located either immediately outside the group of incomplete ridges or by itself in the clear central part of the scales of smelt is taken as the criterion of the annual growth check.

GROWTH

Length and First Year Scale Ridges

Samples of spawning smelt were collected from as many as 12 Miramichi streams at 7- to 10-day intervals from 1949 to 1953 inclusive. Ages, lengths and numbers of first year scale ridges were tabulated according to quarters (8 to 12 days each depending on the season) of each spawning season, late April to early June (Table I). The average lengths of smelt 2, 3 and 4 years old decreased by about 12.5 mm. during the spawning seasons. The fish 5 and 6 years old showed

TABLE I. Average lengths and average number of first year scale ridges of spawning smelt of the Miramichi area, 1949–53 inclusive, arranged according to the quarter of the spawning season in which they were taken.

	1st quarter	2nd quarter	3rd quarter	4th quarter
Age 2 years				
Length, *mm.*	142	135	131	128
No. of ridges	9.7	6.7	4.4	3.1
No. of specimens	2,881	2,886	2,786	3,128
Age 3 years				
Length, *mm.*	164	156	155	153
No. of ridges	7.7	3.9	3.2	2.7
No. of specimens	1,157	1,160	1,319	1,469
Age 4 years				
Length, *mm.*	183	175	172	168
No. of ridges	7.6	4.3	3.2	2.3
No. of specimens	167	125	168	257
Age 5 years				
Length, *mm.*	203	190	189	180
No. of ridges	7.7	5.6	2.5	2.6
No. of specimens	15	7	18	31
Age 6 years				
Length, *mm.*	243	218	197	203
No. of ridges	8.0	5.0	1.0	2.0
No. of specimens	1	1	1	1

an even greater seasonal decrease, but the samples were much smaller. The average number of first year scale ridges in each age-class also declined as the seasons progressed, i.e. the shorter the fish, the fewer the ridges. The average number of first year scale ridges in the "first quarter" of each season shows a decline with advancing age as well.

LENGTH AND WEIGHT

The relationship between length and weight of 9,109 smelt of the Miramichi sampled during the commercial fisheries of 1950–51, 1951–52 and 1952–53 is shown in Table II and Fig. 8. Most of the smelt under 120 mm. in length are immature but some can be differentiated sexually without magnification at lengths down to 105 mm. Maturing smelt are heavier than immature fish of the same length. In samples of 100 fish or more the average weight of females varies little from that of the males of similar length.

LENGTH AND AGE

Samples from 6 commercial seasons, 1949–50 to 1954–55 inclusive, confirm that usually the average length of each age-class in the catch declined as each season progressed (Table III).

Average lengths of year-classes also varied and could be detected from the time they entered the fishery in December at 2– years of age. The 1948 year-class

(age 2– smelt during the 1949–50 season) were the smallest fish and the 1949 year-class (2– smelt in 1950–51) were the biggest. The size-difference between these year-classes persisted as they grew older and were caught as 3–, 4– and 5– fish.

TABLE II. Length–weight relationship of immature, mature male, and mature female Miramichi smelt caught during the 1950–51, 1951–52, and 1952–53 commercial fisheries. Length is measured to the end of the scales on the caudral peduncle; number of individuals is in brackets.

Length range	Average weight in grams			
	Immature	Males	Females	Grand average
mm.	*g.*	*g.*	*g.*	*g.*
80–84	6.0 (10)	...	...	6.0 (10)
85–89	7.8 (9)	...	...	7.8 (9)
90–94	7.6 (10)	...	...	7.6 (10)
95–99	8.3 (6)	...	...	8.3 (6)
100–104	10.9 (18)	...	...	10.9 (18)
105–109	11.6 (55)	...	...	11.6 (55)
110–114	13.6 (182)	14.1 (5)	...	13.6 (187)
115–119	15.2 (285)	15.9 (29)	15.9 (8)	15.3 (322)
120–124	16.8 (229)	17.9 (98)	19.0 (27)	17.3 (354)
125–129	18.3 (110)	20.3 (193)	21.1 (59)	19.8 (362)
130–134	20.9 (43)	23.1 (329)	22.9 (125)	22.9 (497)
135–139	23.8 (4)	25.8 (509)	25.8 (183)	25.8 (696)
140–144	25.3 (5)	28.8 (612)	28.8 (293)	28.8 (910)
145–149	32.1 (3)	32.5 (687)	32.3 (359)	32.4 (1049)
150–154	33.9 (4)	35.4 (603)	35.7 (360)	35.5 (967)
155–159	37.8 (1)	39.5 (552)	39.2 (298)	39.4 (851)
160–164	39.8 (3)	43.7 (489)	43.0 (239)	43.4 (731)
165–169	43.1 (2)	47.5 (404)	47.5 (211)	47.5 (617)
170–174	...	52.2 (253)	52.6 (193)	52.3 (446)
175–179	49.1 (3)	57.7 (178)	58.3 (160)	57.9 (341)
180–184	...	63.9 (92)	64.5 (120)	64.2 (212)
185–189	...	69.4 (60)	70.1 (96)	69.8 (156)
190–194	...	76.2 (52)	75.5 (64)	75.9 (116)
195–199	...	83.8 (19)	84.1 (52)	84.0 (71)
200–204	...	87.4 (9)	90.7 (38)	90.1 (47)
205–209	...	87.6 (3)	98.8 (16)	97.1 (19)
210–214	...	111.9 (3)	104.8 (13)	106.1 (16)
215–219	...	...	114.3 (13)	114.3 (13)
220–224	...	119.0 (1)	119.7 (6)	119.6 (7)
225–229	...	...	135.9 (6)	135.9 (6)
230–234	...	...	128.3 (6)	128.3 (6)
235–239	...	...	139.5 (2)	139.5 (2)
240–244	...	...	...	...
245–249	...	...	132.0 (1)	132.0 (1)

Average lengths of spawning smelt sampled in 1950, 1951 and 1952 are shown in Table IV according to age, sex and first year scale ridges. Average lengths vary each spring depending on the proportion of individuals with different numbers of first year scale ridges included, as fewer ridges mean shorter fish. However, for all ages of smelt and in all years the females were longer on the average than the males. The grand average indicates that this difference increased from 4 mm. at 2 years of age to 24 mm. at 5 years of age.

A comparison of lengths according to age, sex and seasons shows that the average lengths of smelt 2–, 3–, 4– and 5– years caught during the winter commercial season was greater than the average lengths of smelt 2, 3, 4 or 5 years old taken during the spawning season 4 or 5 months later (Table V). The difference in length varied irregularly from 3 to 8 mm. depending on age and sex.

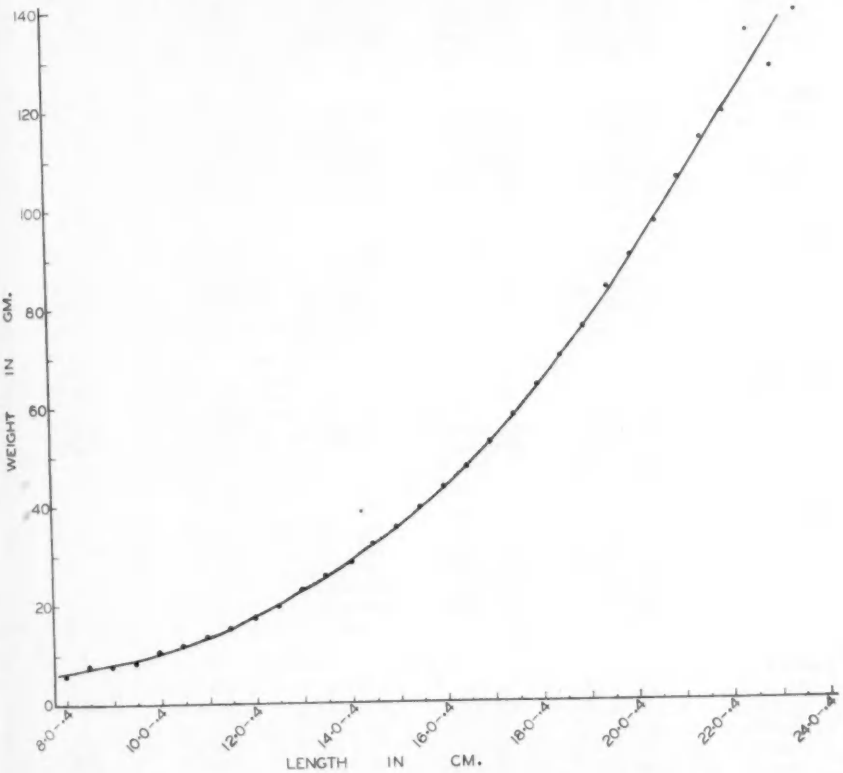

FIG. 8. Weight plotted against length of smelt of the Miramichi, averaged by half-centimetre classes. (Commercial season samples 1950–51, 1951–52, 1952–53.)

WEIGHT AND AGE

Table VI shows the average weights according to ages in samples from the commercial catch during the 4 seasons from 1950–51 to 1953–54. Because of their scarcity in the samples, ages 1– and 6– have not been included in the table. The general average weight of age 3– smelt is 73% greater than age 2– fish; and the 4– fish are about 44% heavier than the 3– fish.

TABLE III. Average lengths of smelt according to ages and months during 6 commercial seasons, 1949–50 to 1954–55 inclusive. (Minus sign after ages means that the fish would not have been the age indicated until the following spring; the number of individuals is in brackets.)

Month	2– years	3– years	4– years	5– years	6– years
1949–50	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
December	138 (1336)	157 (754)	187 (124)	206 (11)	
January	133 (1101)	153 (484)	174 (32)	202 (1)	
February	135 (1135)	154 (421)	182 (33)	187 (2)	
Average	136 (3572)	155 (1659)	184 (189)	203 (14)	
1950–51					
December	149 (928)	165 (588)	176 (148)	217 (13)	
January	145 (819)	163 (400)	172 (107)	219 (1)	
February	145 (896)	166 (309)	176 (63)	181 (3)	
Average	146 (2643)	165 (1297)	175 (318)	210 (17)	
1951–52					
December	143 (1209)	172 (226)	186 (59)	200 (11)	226 (2)
January	141 (1353)	170 (178)	184 (36)	194 (11)	
February	141 (884)	168 (118)	188 (26)	198 (6)	213 (1)
Average	142 (3446)	170 (522)	186 (121)	197 (28)	222 (3)
1952–53					
December	144 (616)	171 (866)	194 (79)	202 (12)	224 (4)
January	139 (792)	167 (770)	187 (32)	193 (3)	
February	141 (552)	167 (401)	190 (26)	226 (1)	212 (3)
Average	141 (1960)	168 (2037)	192 (137)	202 (16)	219 (7)
1953–54					
November	150 (393)	170 (453)	197 (130)	212 (27)	
December	144 (584)	169 (602)	190 (118)	214 (4)	
January	140 (677)	167 (520)	190 (67)	223 (1)	
February	139 (833)	167 (394)	184 (61)	206 (1)	
Average	142 (2487)	168 (1969)	192 (376)	212 (33)	
1954–55					
November	148 (1105)	173 (343)	191 (83)	206 (22)	
December	140 (1108)	168 (394)	190 (71)	212 (15)	233 (1)
January	141 (1001)	165 (442)	185 (77)	216 (13)	
February	141 (1247)	164 (465)	186 (79)	208 (12)	
Average	143 (4461)	167 (1644)	188 (310)	210 (62)	233 (1)
Grand averages					
November	149 (1498)	172 (796)	195 (213)	209 (49)	
December	142 (5781)	166 (3430)	188 (599)	208 (66)	226 (7)
January	140 (5743)	164 (2794)	182 (351)	205 (30)	
February	140 (5547)	164 (2108)	184 (288)	202 (25)	212 (4)
All months	141 (18,569)	166 (9,128)	187 (1,451)	207 (170)	221 (11)
Age distribution (%)	63	31	5	1	<1

TABLE IV. Average lengths of spawning smelt according to age, sex, and first year scale ridges during the springs of 1950, 1951, and 1952. (Number of specimens is in brackets.)

Ridge count range	Age 2 years		Age 3 years		Age 4 years		Age 5 years	
	Males	Females	Males	Females	Males	Females	Males	Females
	mm. *no.*	*mm.* *no.*	*mm.* *no.*	*mm.* *no.*	*mm.* *no.*	*mm.* *no.*	*mm.* *no.*	*mm.* *no.*
Spring 1950								
0–4	128 (622)	131 (255)	147 (1148)	152 (368)	164 (49)	176 (27)	181 (6)	205 (2)
5–9	133 (399)	135 (198)	152 (282)	158 (109)	168 (30)	189 (13)	189 (1)	218 (1)
10–14	140 (349)	141 (224)	159 (78)	168 (45)	179 (6)	197 (12)	(0)	(0)
15–19	145 (45)	148 (24)	162 (5)	(0)	180 (1)	196 (3)	(0)	(0)
Average	133 (1415)	136 (701)	149 (1513)	154 (522)	167 (86)	185 (55)	182 (7)	209 (3)
Spring 1951								
0–4	136 (435)	139 (97)	158 (294)	166 (81)	165 (116)	177 (42)	184 (5)	(0)
5–9	140 (580)	144 (192)	162 (106)	170 (65)	172 (39)	184 (14)	188 (2)	216 (1)
10–14	148 (331)	152 (126)	165 (69)	177 (45)	180 (12)	197 (5)	195 (1)	(0)
15–19	155 (40)	159 (17)	173 (6)	183 (3)	(0)	(0)	(0)	(0)
Average	141 (1386)	146 (432)	160 (475)	170 (194)	167 (167)	181 (61)	186 (8)	216 (1)
Spring 1952								
0–4	125 (474)	128 (122)	155 (382)	161 (64)	172 (89)	181 (22)	181 (22)	199 (4)
5–9	133 (597)	136 (147)	159 (284)	170 (72)	174 (23)	185 (7)	179 (7)	210 (2)
10–14	143 (280)	147 (99)	168 (65)	181 (14)	183 (15)	204 (5)	194 (2)	(0)
15–19	151 (18)	156 (5)	181 (4)	182 (2)	(0)	(0)	(0)	(0)
Average	132 (1371)	137 (373)	158 (735)	168 (152)	174 (127)	185 (34)	182 (31)	203 (6)
Grand average	135	139	153	160	169	183	182	206

TABLE V. A comparison of smelt lengths according to age, sex, and season, 1949–52.

Season	2 years F	2 years M	2 years Diff.	3 years F	3 years M	3 years Diff.	4 years F	4 years M	4 years Diff.	5 years F	5 years M	5 years Diff.
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
Winter 1949–50	140	137	3	162	152	10	194	175	19	214	184	30
Spring 1950	136	133	3	154	149	5	185	167	18	209	182	27
Winter 1950–51	150	145	5	171	160	11	185	168	17	225	200	25
Spring 1951	146	141	5	170	160	10	181	167	14	216	186	30
Winter 1951–52	146	142	4	176	166	10	196	178	18	208	185	23
Spring 1952	137	132	5	168	158	10	185	174	11	203	182	21
Average winter	145	141	5	168	157	11	191	172	19	214	190	24
Average spring	139	135	4	160	153	7	183	169	14	206	182	24
Difference	6	6		8	4		8	3		8	8	

TABLE VI. Average weights (grams) of smelt in commercial catch samples according to age and months during 4 seasons, 1950–51, 1951–52, 1952–53, and 1953–54. Minus sign after ages means that the fish would not have been that age until the following spring.

Age	Number of fish	Dec.	Jan.	Feb.	Averages		Increase over previous year
years	*no.*	*g.*	*g.*	*g.*	*g.*	*ounces*	*%*
2–	7,929	30.5	28.3	28.8	29.4	1.0	?
3–	4,196	52.1	50.5	49.1	50.8	1.8	73
4–	560	74.4	75.1	68.1	73.0	2.6	44
5–	45	92.1	84.7	94.0	90.5	3.2	24

DISCUSSION AND SUMMARY

In the Elbe River of northern Germany, Ehrenbaum (1909) found that the scales of the smelt, *Osmerus eperlanus* L., did not begin to develop until the fish were 45 to 50 mm. long whereas smelt in the Miramichi develop scales at a length of 20 to 25 mm. Masterman's (1913) description of the scales from adult smelt, *O. eperlanus*, and ours of scales from smelt in the Miramichi agree in general. But he indicates that each ridge is outlined from the first as a complete figure and simply becomes more apparent except "at the end of the period of active summer growth" when horseshoe shaped or incomplete ridges form. As in scales of smelt in the Miramichi, these incomplete ridges were surrounded by "a slight scar or junction with the new tissue" and there was no "absorption or abrasion at the edge of the scales" such as occurs in salmon scales at spawning. The fact that Ehrenbaum (1909), Masterman (1913), Creaser (1926), Greene (1930), Beckman (1942), Warfel *et al.* (1943), and Baldwin (1948) made no mention of a shiny line on the central plate and had no difficulty in determining the first year check on their scales is no doubt associated with the early spawning (March and April) in the regions concerned.

Most investigators (Ehrenbaum, 1909; Nordquist, 1910; Masterman, 1913; Van Oosten, 1940; Baldwin, 1948) have found the smelt spawning runs dominated by fish 2 years of age—the youngest fish in the runs. However, Jensen (1949) indicates that in northern Europe most of the fresh-water smelt and some of the brackish water smelt mature in their first year; while the majority of Valday Lake smelt, *O. eperlanus* var. *spirinchus* (Chumaevskaya-Svetovidova, 1945), and the 1923 spawning run in Crystal Lake, Michigan, (Creaser, 1929), were 3 years of age. Most smelt in the Miramichi, like most on both sides of the north Atlantic, reach maturity at the end of their second year.

The decline in size of the different ages of spawning smelt as the season progresses on the Miramichi has not been reported for other regions, though a decline in the average size of all fish as spawning progresses has been recorded by such investigators as Warfel *et al.* (1943). The fact, also, that the average number of ridges on the first growth zone of the scales varies with the length of the fish has not been recorded for smelt of other regions. It was also noted for the first time that the average number of first-year scale ridges declined year by year as the fish of a given year-class grew older (signifying possibly a selective action by the commercial nets on the larger smelt of each year-class). The fact that the fish that are taken in the fishery and that are approaching 2 years of age (or any age) are larger, on the average, than the same year-class taken 3 or 4 months later on the spawning grounds may also be due to the selective action of the commercial nets during the fishery.

When the samples from both the commercial catch and the spawning run are arranged according to age, sex, and number of first year scale ridges, the average length of the females is greater than the average length of males of the same age and ridge count. The difference in length increases as the fish grow older, showing that the females have quite definitely a faster rate of growth than the males.

The length-weight relationship has been determined for fish caught commercially during December, January and February, that is, 3 to 4 months prior to spawning. Proximity to spawning has considerable effect on this relationship, for Nordquist (1910) found that not only did the ovaries make up a greater proportion of the body weight than the testes but that from November to May the ovaries increase from 6% to 18% or 19% of the body weight. Comparisons with the findings of Masterman (1913), Craigie (1927), Beckman (1942) and Marcotte and Tremblay (1948), whose samples were not secured at comparable seasons, are therefore not justified. Other investigators did not record lengths and weights.

The different lengths found in the year-classes as they enter the fishery at 2– years of age may be due to faster growth or variation in the lengths of the growing seasons. A faster growth rate could result from better feeding conditions due to fewer larvae sharing the food or increased food abundance, or both. No information about food abundance is available. However, a comparison of the annual larval production with the average length of these same fish when they entered the fishery (Table VII) at 2– years of age shows that, for the year-classes 1948 to 1951 inclusive, there was no relationship between growth rate and year-class abundance as larvae.

TABLE VII. Comparison of times of spring "break-up" and smelt arrival at head of tide with number of larvae collected at Newcastle Bridge and size of the smelt when they first enter the fishery at 2- years of age.

Year	Ice left river	Smelt arrived head of tide	First 100 larvae collected	Total larvae collected	Size entering fishery
				no.	*mm.*
1948	April 23	April 28	May 25	8,200	138
1949	April 13	April 22	May 15	25,500	149
1950	April 22	April 30	May 23	68,800	143
1951	April 8	April 19	May 19	7,400	144

Table VII does show, however, that the 1949 year-class had the longest fish at 2- years of age and was hatched earliest following an early smelt spawning run and the 1948 year-class had the shortest fish and was hatched latest. Thus the weather and earliness of the spring seasons may have an influence on the size of smelt in the Miramichi as they enter the fishery for the first time.

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Herring Migrations in the Passamaquoddy Region[1,2]

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ABSTRACT

From June 20 to November 21, 1957, 37,495 herring were tagged in the southern part of the Bay of Fundy and Gulf of Maine. These fish were immature and ranged in total length from 14.2 to 18.7 cm. and in age from 1 to 3 years. Recovery of 792 (2.1%) tagged individuals indicated that the herring moved in and out of Passamaquoddy Bay throughout the summer and early autumn. No interchange of herring took place between Passamaquoddy Bay and the coast of Maine or Nova Scotia. Herring moved into Passamaquoddy from as far south as Grand Manan Island and as far east as Point Lepreau. The greatest straight-line distance moved was 55 miles, the mean time before recapture was 12 days, and the longest time 82 days.

INTRODUCTION

The Passamaquoddy region, located on the southwestern shore of the Bay of Fundy, is the centre of an extensive fishery for young herring. Average annual landings from 1937 to 1956 exceeded 50,000,000 lbs. Primary use of these fish is in the production of canned sardines, though utilization also includes fish meal and oil as well as pet food and bait.

There is no evidence of spawning within the Passamaquoddy region and the exact origin of the young herring supporting this extensive fishery is unknown.

Huntsman (1933, 1934) emphasized the importance of hydrographic conditions to the abundance and movements of herring in this area. As herring were taken in stationary brush weirs, Huntsman considered capture as evidence of movement and suggested that herring "be treated as a planktonic form". He concluded that water movements were responsible for carrying the herring into the region and effecting their distribution there.

To provide specific details of young herring movements, a joint tagging experiment was initiated in 1957 by the Fisheries Research Board of Canada and the United States Fish and Wildlife Service. The purpose of this paper is to present the results of the experiment and to discuss the significance of herring movements in relation to time, direction and distance.

MATERIALS AND METHODS

The tag. To initiate a study using tags on sardines, the following requirements were considered: (1) tags had to be external and attached to the head or

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tail, parts of the body which are not canned; (2) tags had to be small and very light in weight because of the size of the fish; (3) tags had to be quickly and readily made in the laboratory; (4) tags had to be conspicuous. The tag used by McKenzie (1950) for smelt fulfilled these requirements. It was made of scarlet "celluloid" 0.01 inch (0.25 mm.) thick. Tags of various shapes were cut out and distinctively marked so that different taggings could be identified. Fig. 1 shows the method of attaching a tag to the operculum of a herring.

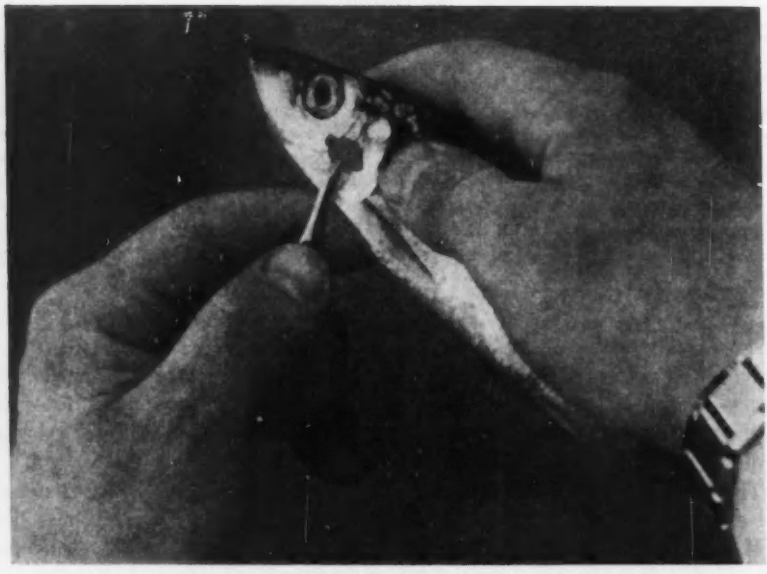

FIG. 1. Attaching a tag to the operculum of a herring. (From McKenzie and Tibbo, 1958)

PRELIMINARY EXPERIMENTS. To test the suitability of this tag for herring, experiments were carried out in the laboratory at St. Andrews, New Brunswick, beginning in November, 1956, by S. N. Tibbo (unpublished data). Thirty-four herring were tagged and an equal number were kept in the same tank as controls. At the end of the first week 10 tagged fish (29%) and 4 controls had died. At the end of the first month 23 tagged fish (68%) and 11 controls were dead. The experiment was concluded at the end of the second month when 4 tagged fish and 9 controls were still alive. No evidence of tag shedding by live fish was seen.

In a similar experiment at Boothbay Harbor, Maine, B. E. Skud and H. C. Boyar (unpublished data) found that cumulative mortalities, including loss of tags, of 51 tagged fish, were 8%, 55%, 84% and 90% in 12, 24, 36 and 48 days respectively. During the same period, cumulative mortalities of 53 controls

were 0%, 20%, 30% and 30%. No records were kept of tags shed by the live fish in the tanks. The tag, although not ideal, was considered to be useful in short term studies of herring movements.

To test recovery, an experiment was carried out by S. N. Tibbo and R. A. McKenzie (unpublished data) at Connors Bros. sardine canning plant in Blacks Harbour on June 5, 1957. Tags were attached to 350 fish entering the plant. With personnel alerted to spot them, 268 (77%) were returned in 3 days, 206 (59%) in the first 2 hours.

FIELD EXPERIMENTS. Fish for tagging were obtained from commercial fishing operations. Great care was taken in handling the fish to insure their return to the water in the best condition possible. Brails and retainers of smooth nylon netting were used to reduce injury from loss of scales. Fish were out of the water for only a few seconds during actual tagging then quickly returned to a net retainer until about 500 had accumulated. Injured fish were removed and the remainder released as small schools rather than as single individuals.

During most of the taggings, samples of fish were taken from the same lots for age and length analyses. Samples taken within the Passamaquoddy region varied in mean total length from 14.2 to 18.7 cm., and in age from 1 to 3 years. Table I shows the length frequency distribution and mean of each sample obtained.

There was no indication that size variation in the tagged fish influenced the results.

TAGGINGS AND RECAPTURES

From June 20 to November 21, 1957, inclusive, 37,495 "sardine" herring were tagged at 15 locations on 17 occasions (Table II). Eight locations were in or at the mouth of Passamaquoddy Bay, two were 25 and 125 miles westward along the coast of Maine, one about 12 miles eastward along the New Brunswick shore, two off southern Grand Manan and two off western Nova Scotia.

A total of 792 or 2.1% were recovered, 738 with complete and 54 with incomplete data concerning time and place of recapture. Only those with complete information are shown in the Figures or considered later in this account.

Distances from tagging sites to recapture positions were measured in straight lines.

The first 5 taggings shown in Table II and Figures 2, 3, and 4 have already been discussed by McKenzie and Tibbo (1958). This tagging of 10,069 herring from June 20 to August 16, 1957, yielded 245 recaptures, 162 of them within 10 days of tagging and the remainder within 80 days. Sixty-six per cent of the recaptures were made within 5 miles of the tagging sites, the others were taken at distances up to 35 miles from the points of release. Some of the recaptures made 30–35 miles away occurred within 6 days of tagging while others were not recovered for 60 days.

Other taggings listed in Table II are described in detail here. Recaptures with incomplete information are not included.

TABLE I. Length-frequency distributions of samples taken from schools of herring that were tagged. Localities marked with an asterisk are outside of the Passamaquoddy region.

Taggings	Length range in millimetres																	
	91–100	101–110	111–120	121–130	131–140	141–150	151–160	161–170	171–180	181–190	191–200	201–210	211–220	221–230	231–240	241–250	251–260	Mean
Moat Island, June 20	...	...	...	...	...	...	2	9	18	11	9	10	5	0	1	1	...	187.0
Harbour de Loutre, June 21	...	...	...	1	15	21	31	24	6	2	...	...	...	...	...	...	...	153.8
Bocabec, July 9	...	...	1	6	32	45	42	37	21	5	1	...	...	...	...	...	...	153.3
New River Beach, July 23	...	1	7	41	55	41	22	18	7	3	4	...	...	...	...	...	...	142.4
Lords Cove, August 22	...	...	...	3	3	19	29	25	10	8	0	1	1	1	...	...	...	160.3
Frost Cove, September 4	1	5	4	8	21	42	41	40	24	6	4	3	0	0	0	1	...	154.6
McDougal's Island, September 5	...	...	5	13	38	53	33	26	17	9	4	1	0	0	1	...	...	151.4
Bucks Harbor,* September 13	...	...	...	1	2	2	10	16	15	19	23	7	3	1	1	...	...	181.4
Harmon Harbor,* October 24	...	2	12	34	44	5	0	2	1	...	...	...	...	...	...	...	...	130.1
Harmon Harbor,* October 30	...	1	6	20	57	7	4	2	1	0	1	1	...	...	...	...	...	146.2
White Head Island,* November 21	...	...	...	...	...	...	...	1	5	18	18	21	14	5	3	...	...	201.0

TABLE II. Recaptures from herring taggings, June 20 to November 21, 1957.

Location	Fish tagged		Recaptures		Total recaptures	
	Date	Number	Complete data	Incomplete data	Number	Per cent
Moat Island	June 20	1,452	13	1	14	0.9
Harbour de Loutre	June 21	1,460	23	7	30	2.1
Bocabec	July 9	2,974	128	22	150	5.0
New River Beach	July 23	2,183	48	10	58	2.7
Pats Cove	Aug. 16	2,000	33	3	36	1.8
Lords Cove	Aug. 21	1,360	39	2	41	3.0
Frost Cove	Sept. 4	2,989	32	1	33	1.1
McDougal's Island	Sept. 5	2,993	61	5	66	2.2
Bucks Harbor	Sept. 13	2,959	2	0	2	0.1
Digby Basin	Sept. 18	1,985	0	0	0	0
Johnson Bay	Oct. 1	2,860	104	3	107	3.7
Bocabec	Oct. 2	2,963	3	0	3	0.1
Cumberland Shore	Oct. 3	2,965	2	0	2	0.1
Harmon Harbor	Oct. 24	461	0	0	0	0
Harmon Harbor	Oct. 30	1,967	250	0	250	12.7
Lear Island	Oct. 30	2,951	0	0	0	0
White Head Island	Nov. 21	973	0	0	0	0
Totals		37,495	738	54	792	2.1

LORDS COVE TAGGING (Fig. 5). On August 21, 1,360 herring were tagged at the Growler weir. Twenty-seven of the recaptures were taken during the first 10 days, 11 within 2 miles of the tagging site, 14 around St. Andrews peninsula and at the head of Passamaquoddy Bay and 2 from Pats Cove, Grand Manan. The remaining 12 recaptures were taken within the next 6 weeks, 2 in the tagging area and 9 at the head of Passamaquoddy Bay. A fairly rapid movement away from the tagging area to the inner part of Passamaquoddy Bay was indicated by these recaptures.

FROST COVE TAGGING (Fig. 6B). On September 4, 2,989 herring were tagged at the Edgar Ritchie weir in Frost Cove, Maine. All recaptures were made more than 2 miles from the tagging site. During the first 10 days following tagging, 20 were recaptured—16 around St. Andrews peninsula and the St. Croix River west of St. Andrews, 3 on the east side of Passamaquoddy Bay and 1 near Lepreau. Of the remainder, 11 were recaptured within another month in the regions indicated above, while 1 was recaptured in Cobscook Bay. Here again, the movement was chiefly to the head of Passamaquoddy Bay with many returns from the St. Andrews peninsula.

MCDOUGAL'S ISLAND TAGGING (Fig. 6A). On September 5, 2,993 herring were tagged at the McDougal's Island weir. Thirty-eight were recaught in the first 10-day period—16 within 2 miles of the tagging site and 22 up to 20 miles away. Fifteen of the 22 were recaptured westward as far as St. Andrews Point and 7 along the shore towards Point Lepreau. The other 23 recaptures were taken during the next 3 weeks—5 within the tagging region and 18 outside of it, all westward around the head of Passamaquoddy Bay as far as St. Andrews. While most of the recaptures were thus from the head of the Bay, a few were from the Bay of Fundy shore almost to Point Lepreau.

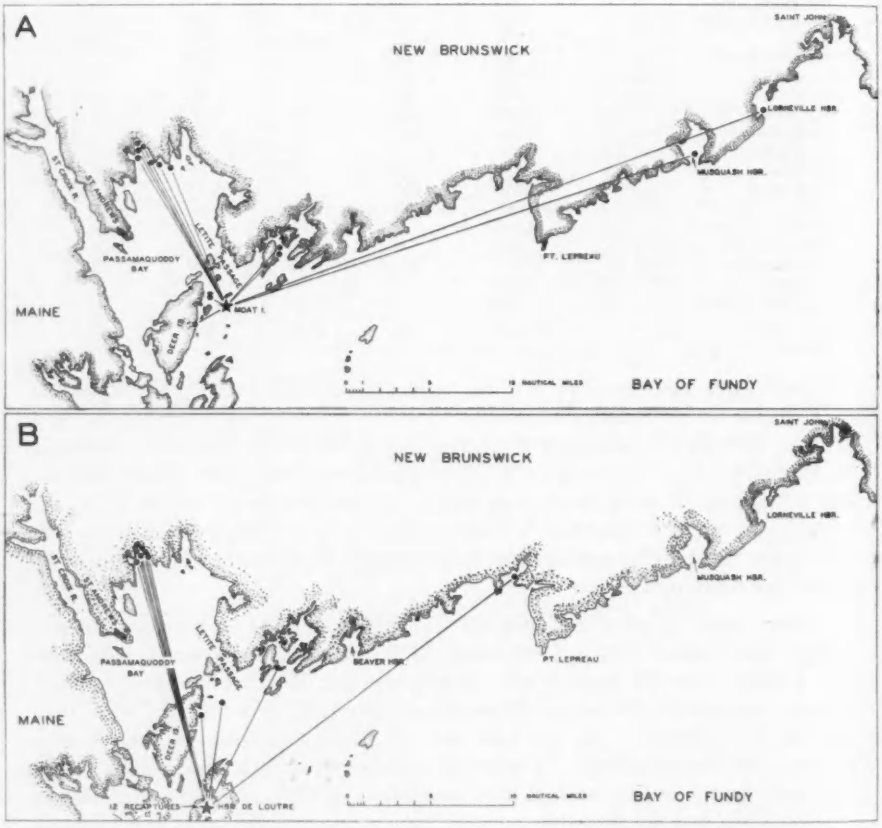

FIG. 2. A. Recaptures of herring tagged at Moat Island on June 20. B. Recaptures of herring tagged at Harbour de Loutre on June 21.

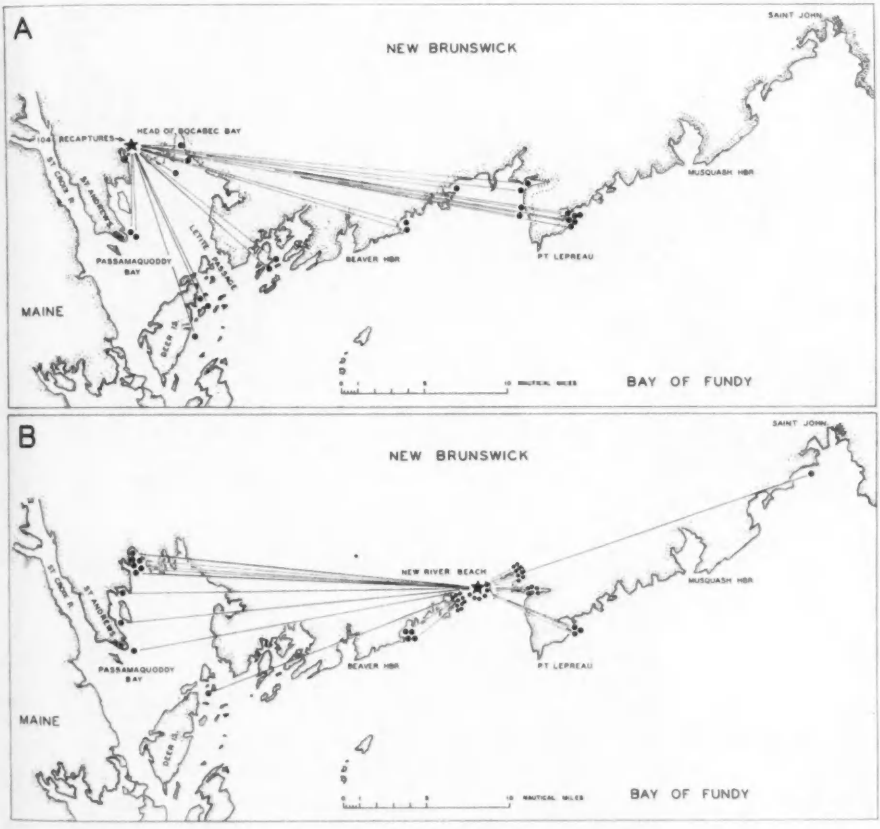

FIG. 3. A. Recaptures of herring tagged at Bocabec on July 9. B. Recaptures of herring tagged at New River Beach on July 23.

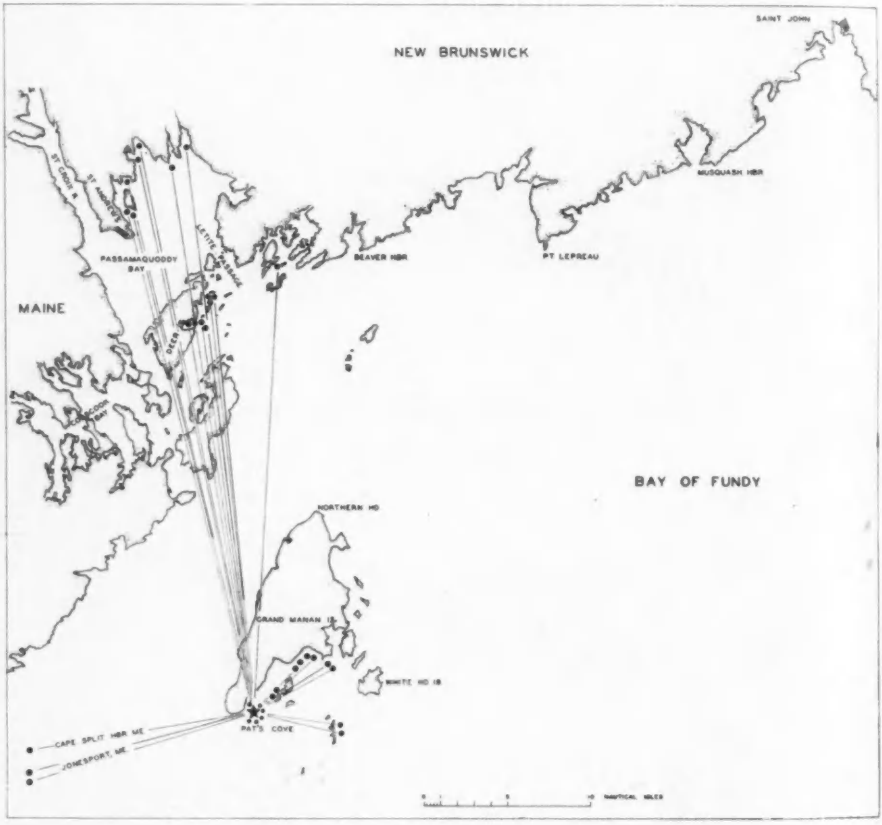

FIG. 4. Recaptures of herring tagged at Pats Cove, G.M., on August 16.

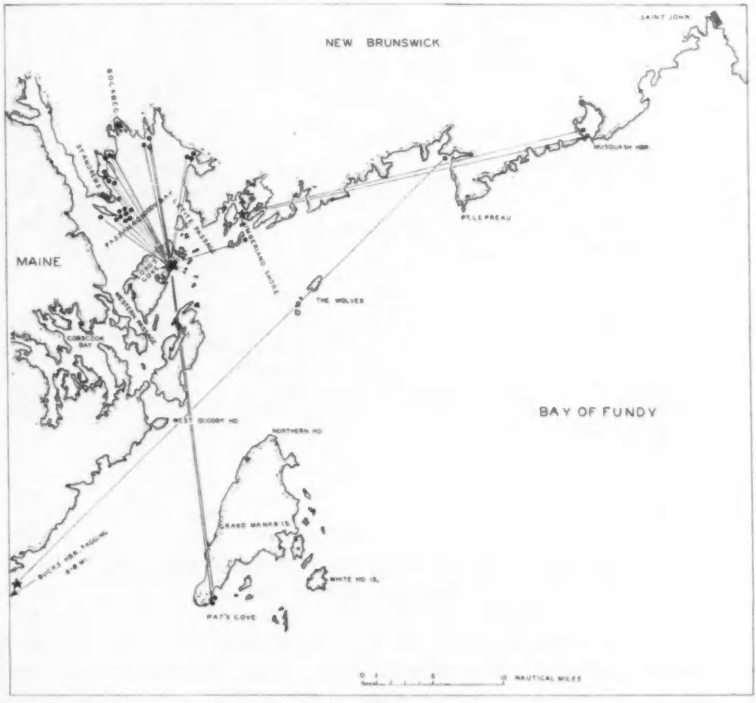

FIG. 5. Recaptures of herring tagged at Lords Cove, August 21; Bocabec, October 2; Bucks Harbor, September 13; Cumberland Shore, October 3.

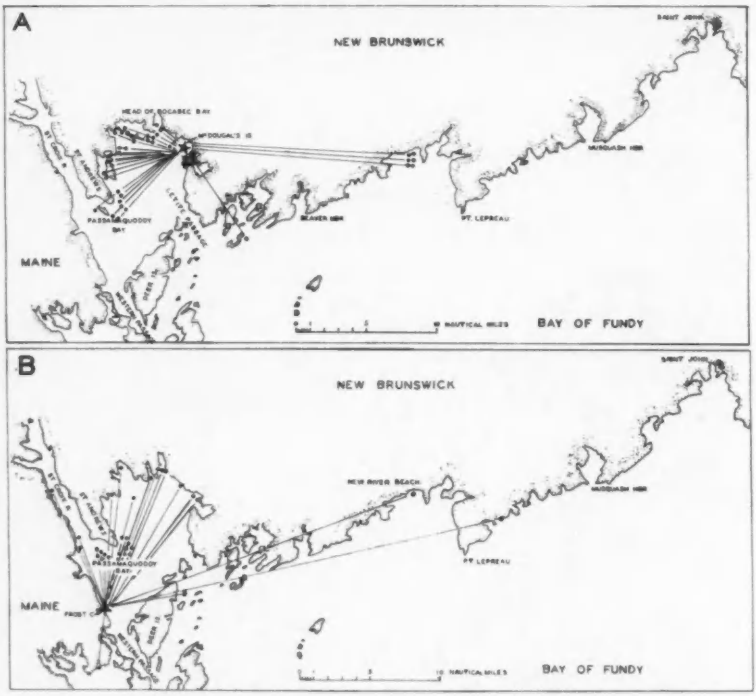

FIG. 6. A. Recaptures of herring tagged at McDougal's Island, September 5. B. Recaptures of herring tagged at Frost Cove, September 4.

BUCKS HARBOR TAGGING (Fig. 5). On September 13, 2,959 herring were tagged on the southwest side of Bar Island in Bucks Harbor, Maine, about 25 miles west of Passamaquoddy Bay. Only 2 recaptures were made—1 not far from the tagging site, while the other was retaken about 50 miles eastward towards Saint John in Lepreau Harbour.

JOHNSON BAY TAGGING (Fig. 7). On October 1, 2,860 herring were tagged at the Jesse Tucker weir, in Johnson Bay, Lubec, Maine. Of the 92 recaptured during the first 10 days, 87 were taken at the tagging site, the other 5 in Cobscook Bay, 6 to 7 miles away. The remaining 12 recaptures were made in the next 2 weeks—4 at the tagging site, 1 in Cobscook Bay, 6 at the head of Passamaquoddy Bay and 1 in Musquash Harbour to the eastward near Saint John. In this tagging also, the movement was into the Cobscook-Passamaquoddy area and to the head of the latter bay.

BOCABEC TAGGING (Fig. 5). On October 2, 2,963 herring were tagged at the Apple Tree weir in the head of Bocabec or Big Bay. The 3 recoveries were within 2 days of tagging and in adjacent weirs.

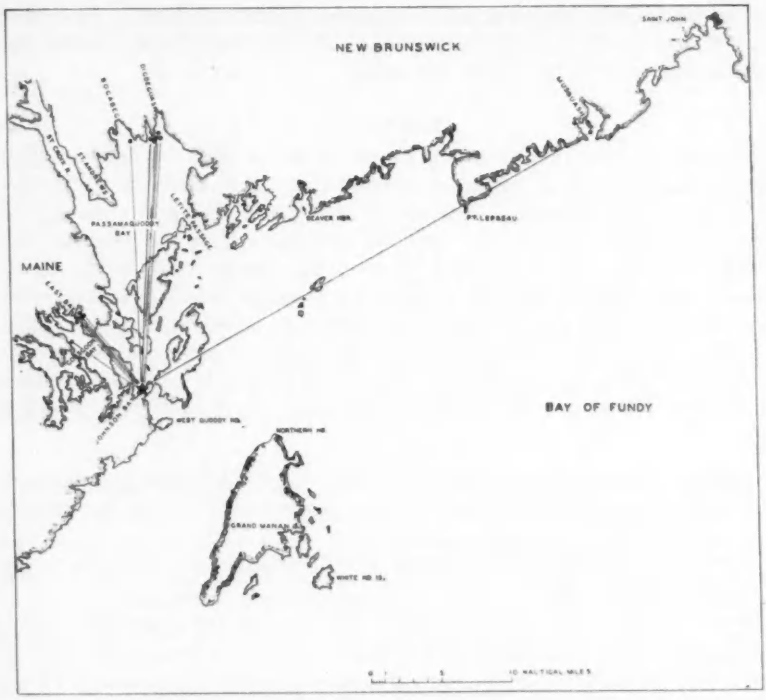

FIG. 7. Recaptures of herring tagged at Johnson Bay, October 1.

CUMBERLAND SHORE TAGGING (Fig. 5). On October 3, 2,965 herring were tagged at the Cumberland Shore weir off Frye or Cailiff Island. Only 2 recaptures were made, both in Musquash Harbour near Saint John, about 25 miles from the tagging site.

HARMON HARBOR TAGGING. No recoveries were made from 461 tagged herring released at Harmon Harbor, Maine, on October 24. However, 250 recoveries were made after a second tagging of 1967 fish on October 30. All recoveries were made on November 6 within a mile of the point of release. Local fishermen believed that strong on-shore winds held fish of the latter tagging in the Bay, whereas offshore winds after the first tagging did not prevent movement out of the bay. Two tag patterns were used in the second tagging and 972 and 995 fish were released. Fish tagged with one pattern were held for at least an hour and released in lots of about 500; fish tagged with the other pattern were held for not more than 10 minutes and released in lots of 25. The number of recoveries was 125 for each pattern and indicated no difference in rate of recapture.

ADDITIONAL TAGGINGS. No recaptures were recorded from 1,985 herring tagged at Digby Basin, N.S., September 18; 2,951 at Lear Island, N.S., near Pubnico,

October 30; and 973 tagged at White Head Island, Grand Manan, November 21. The fact that herring fishing ended in each of these localities soon after tagging probably accounts for the lack of recoveries.

DISCUSSION

Recaptures were considered from the point of view of the distance and direction that the tagged herring moved and the length of time between tagging and recapture. In Tables III, IV, and V and the following discussions, 44 recaptures from the Johnson Bay and 250 recaptures from the Harmon Harbor taggings have not been included because the former were recaught where released within a day and the latter were recaught where released within a week. Other taggings showed that total recoveries varied from 0.1 to 5.0%. Low percentage recoveries may be attributed to tagging late in the fishing season. On the other hand, high percentage returns were made in areas where the concentration of fishing gear was high and the major portions of the catches were made.

EXTENT OF MOVEMENT. Table III shows that 64.2% of the recaptures were made within 5 miles of the points of release. Beyond this distance, the recaptures

TABLE III. Recaptures of tagged herring at 5-mile intervals from points of release.

	Distance, 5-mile intervals												
Taggings	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55–60	Totals
Moat Island	4	7	0	0	0	1	1	...	...	...	...	...	13
Harbour de Loutre	12	3	0	7	1	0	0	...	...	...	...	...	23
Bocabec	108	2	5	3	4	6	0	...	...	...	...	...	128
New River Beach	30	7	0	1	10	0	0	...	...	...	...	...	48
Pats Cove	7	8	0	0	4	4	9	1	...	...	...	...	33
Lords Cove	13	24	0	0	2	...	...	...	...	...	...	...	39
Frost Cove	18	4	8	0	1	1	...	...	...	...	...	...	32
McDougal's Island	42	13	0	6	...	...	...	...	...	...	...	...	61
Bucks Harbor	1	0	0	0	0	0	0	0	0	0	1	...	2
Johnson Bay	47	6	0	6	0	0	0	1	...	...	...	...	60
Bocabec	3	...	...	...	...	...	...	...	...	...	...	...	3
Cumberland Shore	0	0	0	0	0	2	...	...	...	...	...	...	2
Totals	285	74	13	23	22	14	10	2	0	0	1	...	444
Percentage	64.2	16.7	2.9	5.2	5.0	3.2	2.3	0.5	0	0	0.2	...	

TABLE IV. Recaptures of herring made inside and outside of the tagging areas, by 10-day periods.

10-day periods	Recaptures inside (less than 2½ miles)	Recaptures outside (more than 2½ miles)
	no.	*no.*
1st	206	94
2nd	27	60
3rd	15	25
4th to 9th	0	17
Total	248	196

TABLE V. Recaptures of tagged herring at 10-day intervals following tagging.

Taggings	Recaptures per 10-day period 1st	2nd	3rd	4th	5th	6th	7th	8th	9th	Total
Moat Island	0	6	5	0	0	1	0	0	1	13
Harbour de Loutre	8	12	3	...	...	...	...	...	...	23
Bocabec	101	22	2	1	2	...	...	...	...	128
New River Beach	33	7	6	0	0	0	2	...	...	48
Pats Cove	20	6	3	2	0	0	0	2	...	33
Lords Cove	27	3	4	0	4	1	...	...	...	39
Frost Cove	20	9	2	1	...	...	...	...	...	32
McDougal's Island	38	13	10	...	...	...	...	...	...	61
Bucks Harbor	0	2	...	...	...	...	...	...	...	2
Johnson Bay	48	7	5	...	...	...	...	...	...	60
Bocabec	3	...	...	...	...	...	...	...	...	3
Cumberland Shore	2	...	...	...	...	...	...	...	...	2
Totals	300	87	40	4	6	2	2	2	1	444
Percentage	67.6	19.6	9.0	0.9	1.4	0.4	0.4	0.4	0.2	

declined sharply. Only 6.2% were recaptured over 25 miles away. One recapture was made as far away as 55 miles—Bucks Harbor, Maine, to Lepreau Basin, New Brunswick. In some cases, these greater distances were travelled within 6 days of tagging, in others it took as much as 60 days, but, on the average, recapture occurred in 18 days. Of the 285 recaptures within 5 miles of the point of release, 248 were taken within 2½ miles. Table IV shows that in the first 10 days only 31.3% of the recaptures were made beyond 2½ miles of the tagging sites. This percentage increased during successive 10-day periods. After 30 days all recaptures were made beyond 2½ miles.

DIRECTION OF MOVEMENT. There was no apparent seasonal change in the directional movement of the tagged herring. Movements away from the tagging sites were generally not in a single direction. Throughout the summer and autumn months, fish moved both into and out of Passamaquoddy Bay.

Movement into the Bay occurred from points as far east as Point Lepreau and from Grand Manan Island to the south. Of the fish tagged west of West Quoddy Head on the Maine coast, only one was recovered east of Passamaquoddy Bay (Fig. 5). Recoveries in Letite and Western Passages were too few to determine which Passage was used to enter Passamaquoddy Bay. However, the scattering of recoveries made in and about Letite Passage indicated a possible preference for it over Western Passage.

Most recoveries from releases inside Passamaquoddy Bay were made within the Bay itself, in the vicinity of Letite Passage, and east along the mainland shore as far as Saint John. Only two recoveries were made southward to Grand Manan Island and no recoveries were made westward along the coast of Maine. Again, the pattern of recoveries does not indicate clearly whether egress from the Bay was through the Letite or Western Passage.

There were no recoveries in the Passamaquoddy region from taggings carried out in Nova Scotia.

If we assume that the movement of the individuals was not altered by taggings, then the pattern of recoveries suggests that the herring were moving back and forth within the Passamaquoddy region.

DAYS TO RECAPTURE. There was considerable variation in time between tagging and recapture. Over 67% of recaptures were made within the first 10 days, 20% during the next, 9% in the next, and the remainder spread over another 60 days (Table V).

Comparison of the time between release and recovery has been restricted as indicated earlier, and also to experiments which had 10 or more recoveries. The maximum period before recovery was 82 days. In all but one experiment, the mean number of days before recapture ranged from 9 to 15 days. For the exception (Moat Island) the mean was 28 days for the 13 recaptures. Two of these recoveries were made more than 60 days later. The mean number of days from release to recapture for all of the experiments was 12 days. This short period could have been the result of such factors as early loss of tags, tagging mortality or emigration of the tagged fish from the fishing areas. There was no evidence that the tagged fish did emigrate, but laboratory experiments did show high handling and tagging mortality.

As time went on recoveries were not always made progressively farther from the point of release. For example, in the July 9 experiment at Bocabec Bay, one recovery was made as far east as Point Lepreau in 8 days, whereas on July 30 another was made near the tagging site. This phenomenon was repeated in several experiments. Recovery data do not show whether individuals had moved considerable distances and returned to the point of release or whether they had remained in the general vicinity. In many cases, the time lapse was considered great enough for wanderers to have returned to the release site.

SUMMARY

In general the purpose of tagging herring has been to study long distance movements of adult fish. Passamaquoddy taggings provide data on the local movements of immature herring, 1 to 3 years old. Tagging 37,495 of these sardine herring with operculum tags in the southern part of the Bay of Fundy and the Gulf of Maine yielded 792 or 2.1% recoveries. Nearly 50% of the total recaptures were made within 2½ miles and during the first 10 days. Remaining recaptures were spread over distances up to 55 miles, some of which were made within 6 days, some not for 82 days. The mean time from release to recapture was 12 days.

Movements were generally directed in a quadrant extending from the tagging site. Recaptures from taggings inside Passamaquoddy Bay show that movements were mainly to points within the Bay with some towards Letite Passage and as far eastward as Saint John. Recaptures from taggings outside the Bay showed a dominant movement to the head of the Bay with some towards Letite Passage and Point Lepreau. In addition, recaptures from the Grand Manan tagging indicated a movement along the southeastern shore of Grand

Manan as well as westward along the coast of Maine. Though the recoveries indicated considerable movement in the Passamaquoddy region, fish tagged in the Bay were generally recaptured inside, while fish tagged outside also yielded a preponderance of recoveries inside. In addition, the heavy fishery carried on during most of the summer and autumn at the head of the Bay also indicated a concentration of herring there.

Recaptures were made in the Letite area while none were made in Western Passage. This indicated a possible preference for Letite over Western Passage as a means of entering or leaving the Bay.

Apparently no interchange took place between Passamaquoddy Bay and the Nova Scotian shore of the Bay of Fundy. Neither was there any movement from Passamaquoddy Bay to the coast of Maine, but there were 3 recoveries from the Grand Manan tagging along the Maine coast and a single recovery from tagging on the Maine coast eastward at Point Lepreau.

ACKNOWLEDGMENTS

We wish to acknowledge the co-operation of the sardine fishermen and the various plant operators for the return of the tags. We are grateful to the various Canadian Fisheries Officers, especially K. E. Bates, J. P. Cowie, F. W. Durant, and W. C. Hodges, for the purchase and careful recording of tags. Recording of returns in the United States was handled by H. C. Boyar and J. P. Wentworth.

The authors appreciate the extra time and effort given and the enthusiasm with which the technical personnel of the Herring Investigation of the Fisheries Research Board of St. Andrews, N.B., and the U.S. Fish and Wildlife Service at Boothbay Harbor, Maine, carried out the field program.

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The Activity and Catchability of the Lobster (*Homarus americanus*) in Relation to Temperature[1]

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ABSTRACT

The activity (walking rate) of lobsters acclimated to various temperatures increased from 2 to 10°C. and from 20 to 25°C. but was constant between 10 and 20°C. Lobsters acclimated to low temperatures were most active above the acclimation temperature. Those acclimated to intermediate and high temperatures were most active at the acclimation temperatures. Experimental fishing of a relatively constant stock showed that the catch per 100 standard trap hauls (index of catchability) was linearly related to temperature. Slope of line is, however, dependent on stock density. Catchability is shown to be proportional to activity minus a constant. This relationship permits use of catch per unit effort and accumulated catch data to estimate lobster populations.

INTRODUCTION

Where abundant, the lobster is the object of an intensive fishery with the stocks subjected to exploitation rates of 35 to 80% (Wilder, 1947). To provide the biological basis for management of this fishery, long-term population studies have been conducted. One of the more important parameters to be estimated in such studies is the absolute abundance of the stock. Various methods involving the use of tagged or marked individuals are possible but each is subject to error and is often costly. An alternative method suggested by DeLury (1947, 1951) is based on a relationship between catch per unit of effort and the accumulated catch. A basic assumption of this method is that "catchability", defined as the proportion of the population captured by one unit of effort, remains constant throughout the sampling period. General observations, however, suggest that the catchability of lobsters varies with temperature. If so, the relationship between catch per unit of effort and accumulated catch should be modified accordingly.

With lobsters, which are caught almost exclusively in baited traps, catchability is presumably related to activity. As a first approach to a study of catchability the activity of lobsters acclimated to and tested over a wide range of temperatures was measured in a series of laboratory experiments. A more direct index of catchability involved systematic fishing at regular intervals over an 8-month period in an area where the stock was relatively constant. Finally, the two sets of data were examined together to determine the relationship between activity and catchability.

ACKNOWLEDGMENTS

Special thanks are due to Captain W. G. Carson and the crew of the M.B. *Mallotus* from which the experimental fishing was done. Technicians U. J. Walsh and D. E. Graham measured and tagged the lobsters and recorded the observations. Mr. Jyri Paloheimo assisted in the interpretation of the data.

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I. ACTIVITY

Fry and Hart (1948a) demonstrated differences in the activity of goldfish depending partly on the temperature acclimation of the specimen. McLeese (1956) has shown that lobsters have the ability to acclimate and has demonstrated the importance of this in connection with lethal temperatures. It was assumed therefore that acclimation should be considered in the study of activity of lobsters.

Lobsters of both sexes, 23 to 25 centimetres total length, were obtained locally for these tests. They were held in aerated sea water at a series of constant temperatures between 2 and 25°C. until fully acclimated. In 3 weeks at high temperatures lobsters acclimate fully to a temperature change of about 9°C. (McLeese, 1956). However, Brett (1946) found that the rate of acclimation for goldfish depended on the general level of temperature, being slowest at low temperatures. To allow for a possible slower rate of acclimation at low temperatures, lobsters were held for at least 2 months for acclimation to temperatures below 20°C. and for at last 1 month at 20°C. and higher. Temperature control during acclimation was usually within 1°C. of the stated temperature. Variations slightly in excess of these limits occurred infrequently, were of short duration, and had no appreciable effect on the level of acclimation.

The rate of walking in response to a bright light was used as a measure of activity. The rate for one lobster was calculated from the total distance and time taken for 10 trips in a planed soft-wood trough 10 feet long by 8 inches by 8 inches (305 × 20 × 20 cm.) inside dimensions. The walking rate for a given set of test conditions was then taken as the median walking rate of 7 to 15 lobsters. Since the distribution of walking rates for individual lobsters departed from a normal distribution at low and high temperatures, when some animals failed to walk, the median is used rather than the arithmetic mean.

A General Electric RF12 reflector photoflood lamp held 2 feet (60 cm.) directly above the lobster was the stimulus. The light was directed slightly posteriorly, producing a strong gradient of light at the head region of the animal with the darkest area in front of the lobster. The lobster responded by walking forward away from the light. The stimulus was kept essentially constant by moving the light as the lobster proceeded. As shown by preliminary tests, the photoflood lamp produced the most consistent response. In 3 cases lobsters readily completed 10 trips in response to the photoflood lamp. Subsequently they failed to respond uniformly to light sources up to 100 watts but resumed walking when the photoflood lamp was substituted. Lobsters did not respond consistently to either food or diffuse light.

Aerated water at the appropriate test temperature flowed through the trough during the tests. For tests departing from the acclimation temperature, lobsters were transferred to the test temperature at least 1 hour before testing to allow them to equilibrate to the test temperature. The tests were conducted in a darkened room, the tank was painted dull black and the observer was shielded to reduce external stimuli as much as possible.

The results are summarized in Table I. When a series of 10 observations were arranged in increasing order of magnitude, the 3rd and 8th observations were taken as indicative of the range. The 1st and 7th, 2nd and 7th, 2nd and 8th, 3rd and 9th, 3rd and 10th, 4th and 10th, 5th and 11th observations were

TABLE I. Median walking rates of lobsters (ft./min.) for various acclimation and test temperatures. The number of lobsters in each test and the ranges for the medians are given (1 ft./min. = 30.48 cm./min.).

	Test Temperature, Degrees Centigrade						
	2	5	10	15	20	25	28
	Acclimation temperature 2° C.						
Median	7.2	8.9	8.1	4.5	...	...	...
No.	12	9	11	10	...	...	...
Range	6.0–9.5	5.5–13.0	6.5–15.5	0.0–9.5	...	...	...
	Acclimation temperature 5°C.						
Median	8.3	9.5	12.4	11.6	0.0	0.0	...
No.	10	15	9	10	8	9	...
Range	8.0–10.0	8.0–11.0	11.0–14.0	11.5–15.0	0.0–15.0	0.0–9.5	...
	Acclimation temperature, 10°C.						
Median	6.9	12.1	16.4	16.4	14.5	14.6	...
No.	10	10	13	10	10	10	...
Range	6.0–8.0	11.0–14.0	16.5–17.5	12.5–18.0	13.5–16.5	12.0–18.2	...
	Acclimation temperature 15°C.						
Median	0.0	8.1	15.1	17.1	17.3	10.1	...
No.	10	10	10	10	10	10	...
Range	0.0	6.5–9.0	11.4–16.5	16.5–18.5	14.5–18.5	9.0–15.0	...
	Acclimation temperature 20°C.						
Median	0.0	0.0	9.1	14.4	16.5	14.3	...
No.	10	8	7	9	10	10	...
Range	...	0.0–4.5	5.4–10.5	9.6–17.8	14.0–19.0	13.8–17.5	...
	Acclimation temperature 25°C.						
Median	...	...	0.0	14.8	20.6	23.5	19.8
No.	...	...	10	10	10	10	10
Range	...	...	0.0	14.0–16.5	20.0–21.5	22.0–25.0	19.0–23.4

	8° acclimation, tested at 8°C.	22.5° acclimation, tested at 22.5°C.
Median	13.8	21.9
No.	10	10
Range	10.0–15.0	20.0–25.0

used for a series of 7, 8, 9, 11, 12, 13 and 15 observations respectively. These ranges are also confidence limits for the medians, that is the medians will lie within the stated limits at least 9 times out of 10. The actual probabilities range from 0.89 to 0.97, depending on the number of observations (Mood, 1950).

The activity of lobsters fully acclimated to the test temperatures is plotted in Fig. 1. From this curve, activity in relation to acclimation temperature is seen to have 3 phases. As the acclimation temperature increases, up to 10°C. the

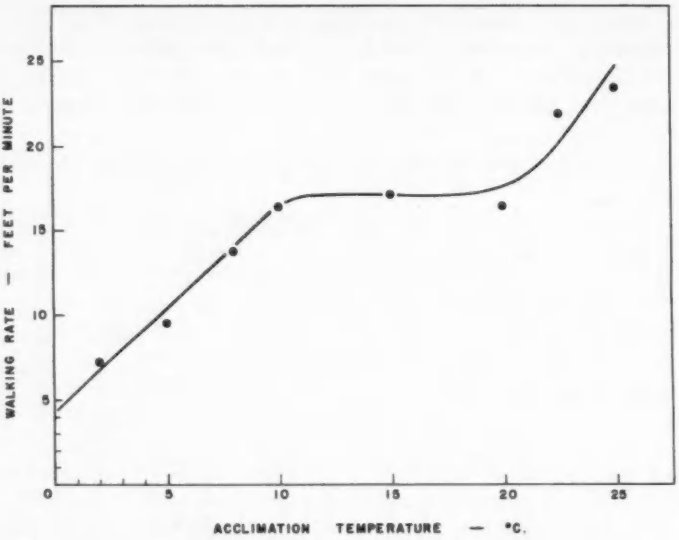

FIG. 1. Activity of lobsters tested at various acclimation temperatures.

level of activity rises rapidly. Activity remains essentially constant for acclimation temperatures between 10° and 20°C. However, the level of activity again increases at acclimation temperatures above 20°C. In general, it has been found that the acclimated activity of fish follows either of two patterns. In one, peak activity occurs at a temperature below the lethal temperature, and in the other, activity progressively increases up to the lethal temperature. These patterns of activity are associated with different relationships between active and standard respiration rates or scope for activity (Fry, 1947; Fry and Hart, 1948a,b; Graham, 1949). The pattern of activity for the lobster, with its rapid increase in activity at temperatures above 20°C., appears to differ from both of these patterns.

The activity of lobsters exposed to sudden temperature changes both upwards and downwards from the acclimation level is shown in Fig. 2. Arrows show upper lethal temperatures and estimated lower lethal temperatures (McLeese, 1956).

Lobsters acclimated to low temperatures (2° and 5°C.) are capable of moderate activity only, regardless of temperature, and attain maximum levels of activity (9 and 13 ft./min.) at temperatures a few degrees above the acclimation temperature. Those acclimated to intermediate temperatures (10°C.) are inactive at low temperatures and attain maximum levels of activity (16 to 17 ft./min.) at the acclimation temperature. For lobsters acclimated to high temperatures (15 to 25°C.) activity is curtailed at low temperatures but reaches a maximum at the acclimation temperature. Activity falls rapidly at higher temperatures, presumably being zero at the upper lethal temperatures.

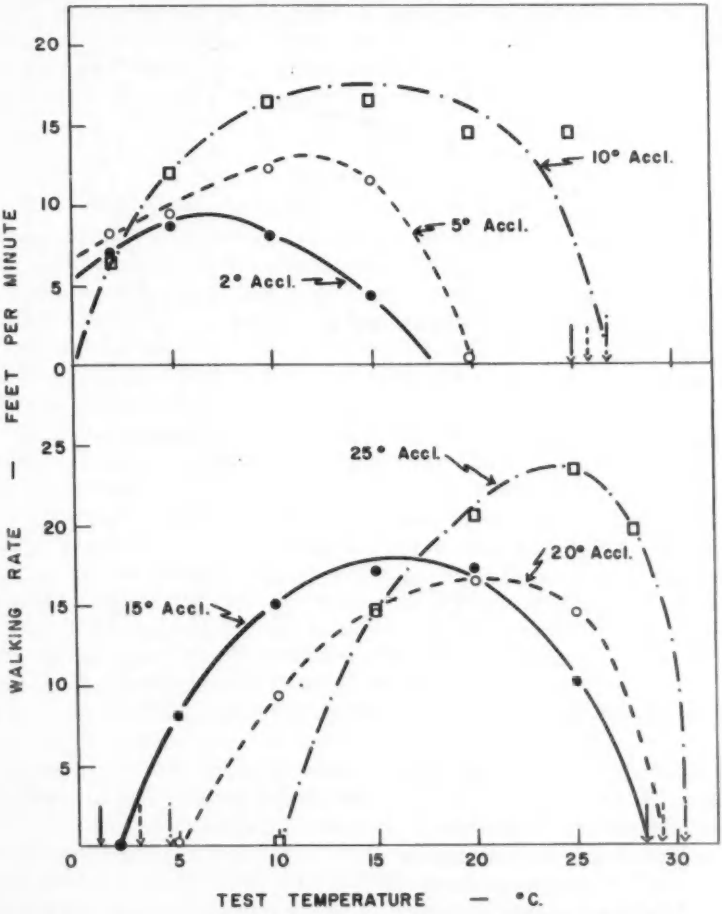

FIG. 2. Activity of lobsters acclimated to various temperatures and tested at a series of temperatures. Arrows on the abscissa indicate upper and lower lethal temperatures.

Brett (1956) pointed out the importance of sufficient activity at near lethal temperatures for continued existence of the animal. Activity as expressed by walking rate is closely related to the ability to feed, compete and to escape predation, all factors necessary for continued survival of the lobster. The temperatures at which activity becomes zero at the various acclimation levels have been plotted on the thermal tolerance diagram (Fig. 3) for the lobster (McLeese, 1956). The diagram encloses temperatures which the lobster can tolerate indefinitely. The area within the diagram is divided into a large zone of activity

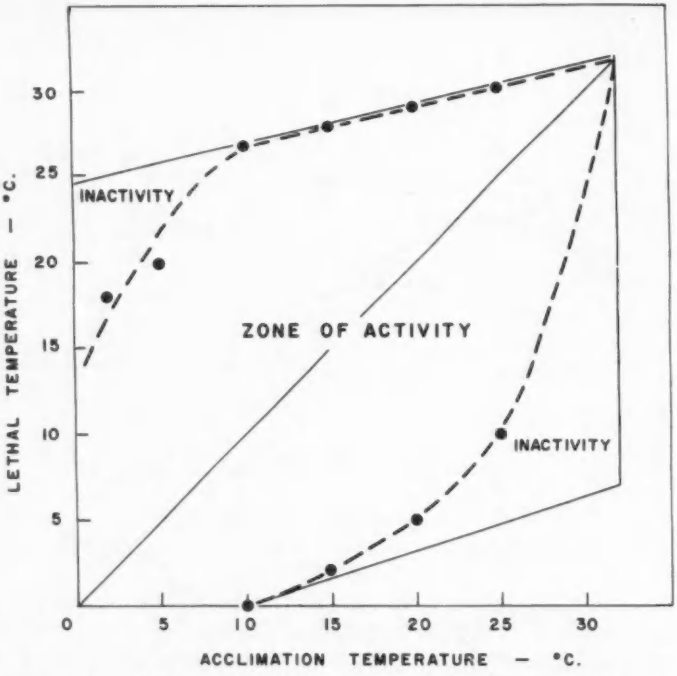

FIG. 3. Thermal tolerance diagram for the lobster showing zones for activity and inactivity. Circles show temperatures of zero activity.

in the central region and two smaller zones of inactivity near the margins. Continued existence of the lobster would not be possible in the zones of inactivity although the temperatures themselves are not lethal.

Throughout this discussion it has been assumed, if not demonstrated otherwise, that activity becomes zero at the lethal temperatures. The lethal temperatures as used here define the zone of temperatures beyond which animals cannot live indefinitely. They can live for short times at lethal temperatures, these times being called resistance times by Fry (1947), but any activity beyond these temperatures would be of short duration and is considered to be zero in this paper. The zone of activity may be interpolated above and below the range of experimental points since activity at the ultimate upper and lower lethal temperatures—the highest or lowest level to which the lethal temperatures can be raised or lowered by thermal acclimation—will be zero. The ultimate upper lethal temperature is 32°C. The ultimate lower lethal temperature, although not experimentally determined, can be taken as the freezing point of sea water, approximately –1.8°C.

Lobsters acclimated at 10 to 15°C. show the greatest range of temperatures for activity. With a rise or fall in acclimation, the range of temperatures for

activity decreases and finally reaches zero at the ultimate upper and lower lethal temperatures. This picture of the zone for activity is dynamic rather than static, because temperature changes departing from the acclimation levels will be accompanied by continual changes in acclimation.

II. CATCHABILITY

The limited stock of lobsters off the St. Andrews Biological Station in the estuary of the St. Croix River is relatively unattractive to commercial fishermen. Although the official lobster season extends from November 15 to June 24, commercial lobster fishing in this immediate area is usually limited to 5 or 6 boats that fish a few traps for several weeks in the fall and spring. The lobster population although small is relatively constant in comparison with areas where the fishery is intense. A further advantage of the area is that it is well sheltered and fishing is possible most days.

From mid-September to mid-April, 35 to 40 traps were fished for 6-day periods at approximately monthly intervals. The wooden traps were a type commonly used in the area and were equipped with a fishing head of hand-knitted nylon at one end and with one inner parlour head. They were approximately 42 inches (107 cm.) long, 26 inches (66 cm.) wide and 18 inches (46 cm.) high, outside dimensions. Lightly salted, sardine-size herring were used as bait throughout the experiment. The traps were set in 2 lines about 1 nautical mile (1.8 km.) long running parallel to and about 200 yards (180 m.) and 500 yards (460 m.) off shore. The inner line was set in 5 to 8 fathoms (9 to 15 m.), the outer in 10 to 16 fathoms (18 to 29 m.).

During the September fishing period the traps were deliberately moved about in an effort to find lobsters. For all subsequent fishing periods the traps were set as consistently as possible on the same grounds. As each trap was fished each day the condition of the trap was noted, the bait renewed, the lobsters measured, tagged, and promptly released close to the point of capture. Once or twice each day the bottom water temperature was taken with a reversing thermometer at an average depth of 10 fathoms (18 m.).

During the experimental fishing 265 lobsters were caught. Their carapace length, measured from the eye socket to the posterior margin of the carapace, ranged from 2.1 to 6.2 inches (5.3 to 15.7 cm.) and averaged 4.0 inches (10.2 cm.). Of these, 26 were recaptured in the experimental gear once, 3 were recaptured twice and 1 was recaptured 3 times to give a total of 35 recaptures. Commercial fishermen, who fished from November 15 to December 14 only, caught and removed 27 of the tagged lobsters.

For the 35 recaptures in the experimental gear, the average time between liberation and recapture was 25 days. The average straight line distance between release and recapture points was 0.1 nautical mile (0.2 km.). The 27 tagged lobsters returned by the commercial fishermen were reported to be free on the average for 27 days, and to have moved an average of 0.5 nautical mile (0.9 km.). The limited distribution of the experimental gear undoubtedly leads

to an underestimate of the average movement, whereas inaccuracies in the fishermen's reports tend to overestimate it. It seems probable that the estimate of 0.3 nautical mile (0.6 km.) based on all recaptures, approximates the true average movement.

The tagged lobsters indicate that the number of catchable-sized lobsters in the experimental area is unlikely to be seriously affected by movements into or out of the area. Since moulting occurs principally during the summer months, recruitment through growth is unlikely to affect the numbers appreciably during the experimental period. Of 223 lobsters tagged to November 9, commercial fishermen caught 26 (11.6%) from November 15 to December 14 and presumably brought about a proportionate reduction in the stock. Natural mortality is believed to be low among the sizes of lobsters under consideration, particularly during the cold water period, and is assumed to have only a minor effect on the stock during the experimental period.

TABLE II. Catchability index of lobsters (adjusted catch per 100 trap hauls) in relation to temperature.

Period	Trap hauls	Catch	Catchability index	Average bottom temperature
	no.	*no.*	*no./100 hauls*	°C.
Sept. 16–24/57	183	50	27.3	12.4
Oct. 7–12/57	175	103	58.8	11.5
Nov. 4–9/57	176	98	55.7	9.8
Dec. 9–14/57	175	26	16.6	6.5
Jan. 13–18/58	171	4	2.6	4.0
Mar. 10–17/58	177	8	5.1	2.8
Apr. 14–17/58	179	11	7.0	3.6

The catch and effort figures, together with average bottom water temperatures, are summarized in Table II for each fishing period. Traps not in fishing order when hauled are not included in the total. The catch includes recaptures. The catch per 100 standard (24-hour set) trap hauls is taken as the index of catchability. For the fourth and subsequent fishing periods the indices have been adjusted to allow for the estimated 11.6% reduction in stock by the commercial fishery. The low September index is not fully understood. The new, previously unused traps may have, as fishermen believe, adversely affected the catch. Some effort expended in September in searching for lobsters was relatively ineffective. Late summer moulting may also have reduced the September catch. In any case the September data are believed to be atypical and are not considered further. The data plotted in Fig. 4 indicate a linear relationship between catchability index and temperature over the range 3 to 12°C.

DISCUSSION

Although the catch per 100 standard trap hauls, used as an index of catchability, is linearly related to temperature over the range 3 to 12°C., the slope of the line depends on the stock density. Because of this, although the relationship is of general importance, it is not of direct applicability. The numerical

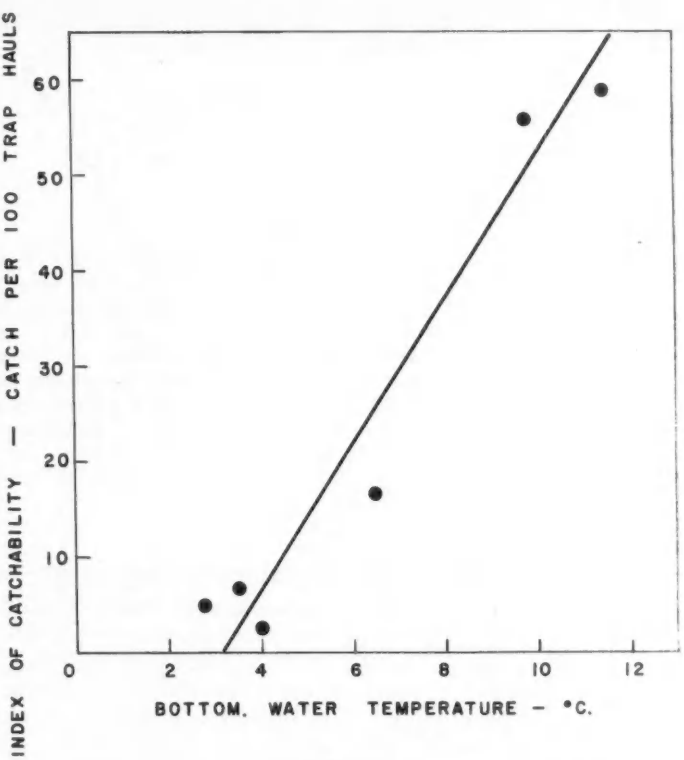

FIG. 4. Catchability of lobsters in relation to temperature.

values for such lines must be determined separately for each stock. However, it appears from Fig. 1 that a linear relationship between activity and temperature holds up to a temperature of 10°C. or more. This relationship is presumably characteristic of the species and should be of general applicability. To determine the relationship between activity and the catchability index, levels of activity corresponding to the average bottom temperatures listed in Table II have been interpolated from Fig. 1. These activity readings were then plotted in Fig. 5 against corresponding catchability indices. The relationship between activity and the catchability index is significant ($r = 0.974$, $P = 0.01$) and appears to be linear. According to this relationship the catchability index is proportional to activity minus a constant. This constant has been estimated graphically at 8.2. Observations based on the commercial winter fishery in southern Nova Scotia suggest that this figure is somewhat too high for that population.

The proportional relationship between activity and the catchability index can be used to correct catch per unit of effort data for varying catchability. Such corrections permit the use of the relationship between catch per unit of effort and accumulated catch for estimating lobster populations.

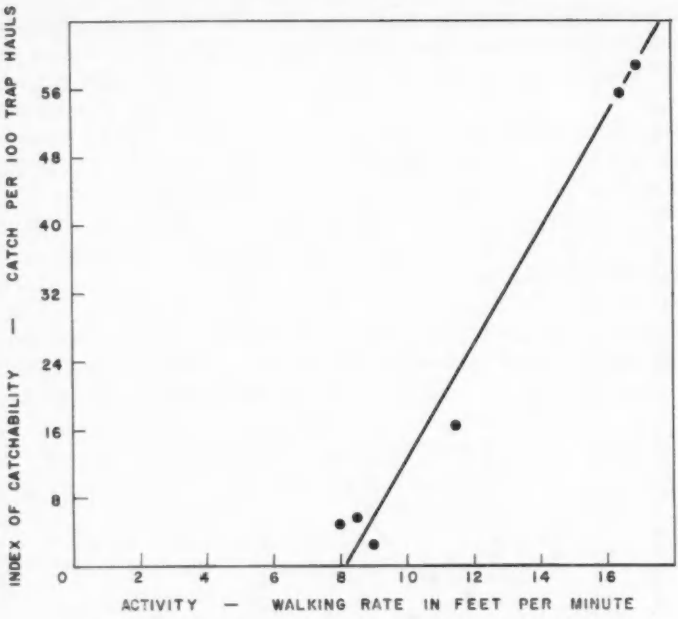

FIG. 5. Catchability of lobsters in relation to activity.

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Trial Control of the Greater Clam Drill (*Lunatia heros*) by Manual Collection[1]

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ABSTRACT

Soft-shelled clams (*Mya arenaria*) 38 mm. long were planted 172 per m.^{2} in three 10 m.^{2} plots in a sandy flat where none occurred naturally but where there were 6 drills per m.^{2} feeding on mussels (*Mytilus edulis*). After plantings, at least 300 drills entered each plot daily. After 12 days clam survival was only 19% in the plot where there was no protection; 31% where soil was raked before planting and exposed drills removed (84% efficient); 34% where this pre-planting clearance was combined with 8 post-planting, low-tide, manual collections of surfacing drills (3% to 5% efficient). These intense efforts had little effect and would be unjustified on public beds even if much more effective. Drills kill more than half their prey without boring their shells. A higher proportion of the drill population comes to the surface by night (6%) than by day (3%) and small drills are unexplainably scarce.

INTRODUCTION

For 50 years people have been trying to cultivate soft-shell clams (*Mya arenaria*) on the Atlantic coast (Mead and Barnes, 1903; Belding, 1931; Medcof, 1947; Turner, 1951). Everyone seems to have recognized the need for protecting the "farmed" shellfish from their natural enemies. These include certain snails, called "clam drills", which drill holes in the shells and eat clams. Some townships in Massachusetts were so impressed with the importance of drills that for several years they offered bounties for their collection. Indeed their shellfish wardens still collect and destroy drills as part of their prescribed duties. There, *Polinices duplicatus* Say and *Lunatia heros* Say (nomenclature according to Abbott, 1954) are the common drills.

When clam farming trials were begun in the Maritime Provinces in the 1940's it soon appeared that 2 species were present here too, the greater and lesser clam drill, *L. heros* and *L. triseriata* Say. These occurred in flats that were well stocked with clams and on others that were barren.

Archaeological evidence suggested that some of the areas which were barren of clams had once been well stocked. For example, Holts Point in Passamaquoddy Bay near St. Andrews, N.B., (45°09′ N. Lat., 66°59′ W. Long.) had no clams. But excavation of kitchen middens on the shore opposite the flats showed that Indians camped there regularly and used large quantities as food. We assume that these clams were dug opposite the encampment from what has since become a barren flat.

When we first visited Holts Point in 1947 we were surprised to find no clams. Physical conditions seemed ideal so we looked for a biological explanation

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for their absence. At that time the green crab (*Carcinides maenas*), one of the clam's worst enemies, had not yet invaded Passamaquoddy Bay. The only predator we could find was the greater clam drill. But it was so abundant that we thought it might account for the absence of clams.

Exploratory experiments were carried out to see if these drills really were important in keeping the clam population down. A more involved control experiment was also performed to assess manual collection of drills as a device for protecting clam stocks planted there artificially during farming trials.

Assistance from Mr. J. S. MacPhail and Dr. M. E. C. Giglioli is gratefully acknowledged.

EXPERIMENTAL AREA

Holts Points flat lies in a protected cove. It is surrounded by a steep shingle beach approximately 200 feet (60 m.) wide sloping 10° to 15° from the horizontal. The upper 140 feet of shingle is bare stones (Fig. 1) but below this the stones are covered with rock weeds (*Fucus* and *Ascophyllum*) to the edge of the flat. Along the lower edge of the shingle on the eastern side of the cove, there was a dense growth of small mussels (*Mytilus edulis*) mostly less than 1½ inches (38 mm.) long.

The transition from shingle beach to flat proper is sudden and the flat itself slopes gently seaward at about 2 to 5° from the horizontal. Its surface is smooth, and its soil a firm sand, with a small amount of silt mixed in. At low spring tides (about datum level) approximately 1½ acres (0.6 hectare) of this flat is exposed. It forms an arc parallel to the edge of the shingle and roughly 250 feet (75 m.) wide.

As an experimental area the flat has the disadvantage of being so low that it is not fully exposed at low neap tides. When Saint John, N.B., water levels, as described in Canadian Hydrographic Service's Atlantic Coast Tide and Current Tables, fall to about 2 feet above datum, the upper part of the flat is exposed for about an hour. However, at low spring tides (datum or lower), it is exposed for 2 to 3 hours. Most observations conducted were possible only in the brief periods of exposure.

Tidal range in this area varies from 23 feet at neaps to 28 feet at springs. Records show that summer salinities normally vary only from 30 to 32‰ and water temperatures from 11.0° to 17.0°C. The area is almost never ice-bound in winter.

Sand dollars (*Echinarachnius parma*) were common just below the lowest low-water mark. At the northwest corner of the flat, mussels (*Mytilus edulis*) were common in a small area at the transition between the flat proper and the shingle beach. Amethyst gem clams (*Gemma gemma*) which are so common in many of our sandy areas were not found there. Other small bivalves that burrow in sand were rare. No lesser clam drills were found although they are common on higher flats in the region.

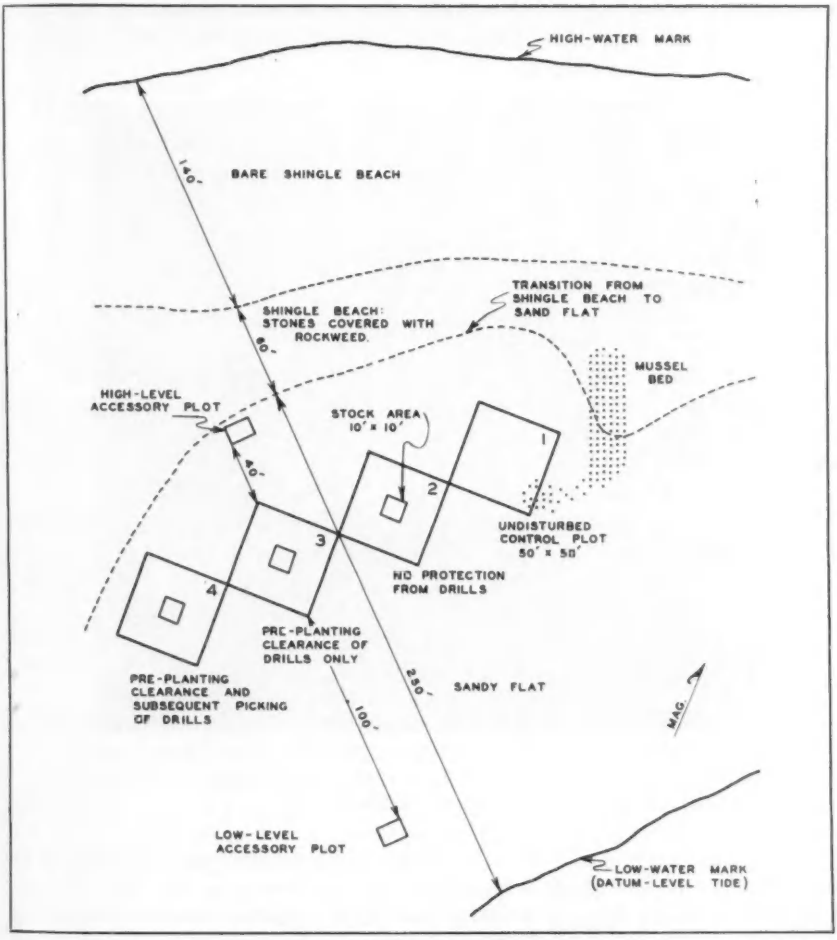

FIG. 1. Lay-out of 1949 experimental plots, Holts Point.

EXPLORATORY EXPERIMENTS

On July 10, 1948, approximately 4,000 clams with an average length of 1½ inches (38 mm.) were planted 16 per ft.^{2} (172 per m.^{2}) in each of 3 plots at different levels on the low barren sandy flat. When the plots were dug 15 days later 75% of the clams in the uppermost plot, 90% in the intermediate and 100% in the lowest, were dead. Drilled shells were scattered on the beach surface for several yards about the plots and live greater drills 20 to 40 mm. in shell height were found buried in the sand a few inches below the surface. Some were

busy drilling or feeding on clams which they held firmly grasped in the foot. A night visit was impressive. Drills were surfacing everywhere and some were feeding at the surface (Fig. 2).

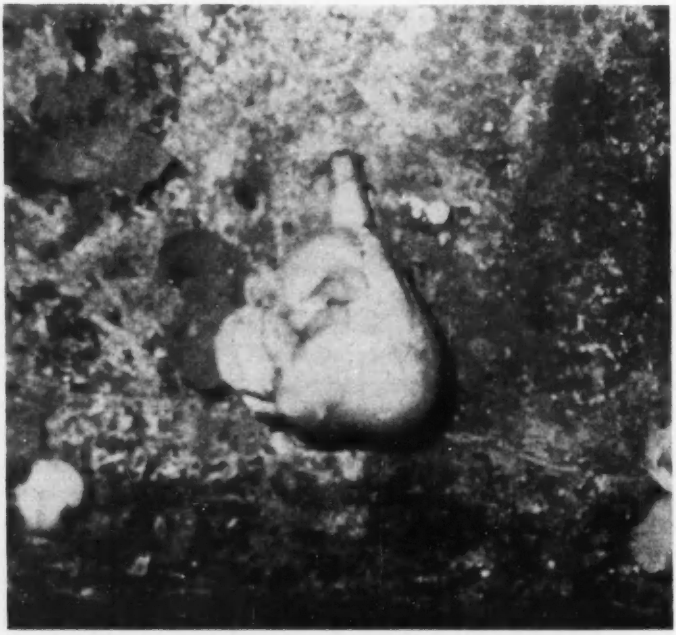

FIG. 2. Night feeding by the greater clam drill on the surface of the sand, at Holts Point. The clam's siphon shows clearly but other parts are hidden by folds of the drill's foot.

A similar planting of 100 1½- to 2-inch clams in each of 4 adjacent plots was made on the site of the intermediate plot on December 28, 1951. The air temperature at the time of planting was 10°F. (–12°C.) and a film of ice formed over the surface of the flat soon after it was exposed by the receding tide. On the next 2 days air temperatures fell to minima of –4° and –6°F. (–20 and –21°C.). Thus the clams were exposed to freezing conditions before they could establish themselves very deep in the soil. Later these plots were dug and the soil sifted through quarter-inch (7 mm.) mesh wire screens to recover surviving clams and any drills that might be attacking them. Table I records results. Judging from January and February entries planting mortalities averaged 30%. In considering April and May entries, therefore, only mortality in excess of 30% is attributed to predation by drills.

These agree with findings of Sawyer (1950) and Hanks (1952) and show that clams have some respite from drill attacks during colder months and that their plight is not as bad as the 1948 experiment alone would suggest.

TABLE I. Recoveries of living clams and of drills from 4 adjacent plots at intermediate beach level, each planted with 100 clams on December 28, 1951 and dug in 1952; Holts Point.

Plot No.	Digging date	Living clams	Mortality from drills	Drills	Remarks
		no.	%	*no.*	
1	Jan. 24	69	1	4	1 drilled shell
2	Feb. 23	71	0	2	No drilled shells
3	Apr. 23	53	17	5	A few drilled shells
4	May 26	40	30	3	Numerous drilled shells; many drills on surface

CONTROL EXPERIMENT

DESIGN OF EXPERIMENT

This experiment was conducted in 1949 to discover if manual collection of greater clam drills could substantially improve survival of planted seed clams. Four uniform plots, each 50 feet (15.2 m.) square, were marked out with wooden stakes as shown in Fig. 1. Plot 1 was left as an undisturbed control area. In the centre of plots 2, 3 and 4, a stock area 10 feet (3.1 m.) square was staked out and planted with clams. Observations were made to see what happens:

1. to clam drills under ordinary conditions on ground that is unpopulated by clams;

2. to clams that are not protected from drills in any way;

3. to clams that are protected by pre-planting clearing of drills from the 50- by 50-foot plot; and

4. to clams that are protected by pre-planting clearing as in 3, and further protected by subsequent periodic manual collection of surfacing drills.

Because it seemed probable that behaviour of drills in these plots would be affected by experimental observations, 2 accessory plots 4 feet (1.2 m.) by 7 feet (2.1 m.) were set up at a high and low level (Fig. 1). There was a 2-foot (0.6 m.) difference in their beach level. After planting, these plots were not even walked over during the experiment.

METHODS AND PROCEDURE

COUNTING SURFACING AND HUMPING DRILLS. Records were made of numbers of snails found on the surface of plots. These, with counts of total populations, were expected to have future usefulness for judging levels of drill infestation of any clam ground from results of surface inspection. Preparatory to surface counting in any plot, either by day or night, codline was strung to the 4 corner stakes. The surface was then examined in transverse strips approximately 5 feet wide by slowly walking across the plot. To avoid overlapping or incomplete coverage the observer carried a stick the tip of which was allowed to mark the outer boundary of each strip examined. This system was especially useful at night when work was done by flashlight.

All drills that could be found were collected in buckets and counted after each plot was covered to avoid counting errors. Sometimes drills were surfacing

TABLE II. Relative efficiency of various daytime methods for clearing drill-infested areas as shown by counts for 8 areas, each of 1 yd.² (0.8 m.²), in plots 1 and 2, June 26, 1949.

	Area No.	Picking (initial)	Raking after picking	Cultivating after picking	Extras by final screening	Total
Plot 1	1	1	4	...	1	6
	2	1	...	1	5	7
	3	2	8	...	2	12
	4	0	...	3	1	4
Plot 2	1	0	4	...	1	5
	2	0	...	6	2	8
	3	0	2	...	0	2
	4	0	...	1	0	1
Totals		4	18	11	12	45

and partly or wholly exposed above the beach surface. Sometimes they were buried but close enough to the surface to produce a noticeable hump in the sand. Occasionally separate records were kept of surfacing and of "humping" drills. Counts of surfacing drills were then reported as such but counts of humping drills were pooled with counts of surfacing drills and the totals were listed as collected drills in tabulated records. Such records for plots 2, 3 and 4 for the period July 6 to 12 are compiled in Table IV, below.

Collected animals were returned to their plots by scattering them in a pattern similar to that observed during collection or dumped on shore above high-water mark to die.

Separate counts were sometimes made of drills found surfacing in a stock area and in the rest of a plot. Stock area counts were recorded as such but rest-of-the-plot counts were pooled with those for stock areas and recorded in tables as whole-plot counts.

INITIAL COMPARISONS OF PLOTS. Drill populations in the 4 plots were compared by counting surfacing drills before plots 3 and 4 were cleared for the experiment. Results are listed in Table III for morning and evening low tides on June 27 and for the morning tide on June 28. Data are sketchy but they suggest that population densities in plots 2 and 3 were about equal and less than half those in plots 1 and 4.

Comparison of plots 1 and 2 is possible from counts made during pre-planting visits on June 29, 30 and July 1 (Table III). Drills were being removed then from plots 3 and 4 but plots 1 and 2 were undisturbed except for counting. Plot 2 had roughly half the drill population of plot 1.

Comparison of plots 3 and 4 is possible from total numbers of drills collected and destroyed June 28 to July 1 (Table III) There were roughly 1½ times as many in plot 4 as in plot 3.

The above comparisons agree very well. Presence of mussels near plot 1 might account for high counts there because drills eat mussels. But there is no apparent reason for high counts observed in plot 4.

TABLE III. Counts of drills in experimental plots during preliminary observations (June 27) and clearing operations (raking, picking and destroying in plots 3 and 4, starting June 28). The estimated initial population, shown in the last line, is based on a raking efficiency of 84%.

	Plot 1	Plot 2		Plot 3			Plot 4		
	Surfacing	Surfacing		Surfacing		Collected and destroyed	Surfacing		Collected and destroyed
Date and time	Whole plot	Whole plot	Stock area	Whole plot	Stock area	Whole plot	Whole plot	Stock area	Whole plot
June 27, 0500–0800	85	29	1	30	0	...	41	2	...
June 27, 1730–1930	68	11	0	...	...	...	83	7	...
June 28, 0630–0930	37	14	1	11	0	...	29	1	1,076
June 29, 0700–1000	...	...	...	16	0	425	7	0	...
June 29, 1800–1930	110	59	...	...	...	...	...	...	...
June 30, 0700–1030	37	27	...	18	0	267	27	7	226
July 1, 0830–1100	75	26	...	25	...	315	28	0	130
Average	69	28	1	20	0	...	36	4	...
No. raked	...	...	...	...	...	1,036	...	...	1,432
No. left	...	...	...	...	...	200	...	...	300
Estimated initial population	*ca.* 1,700	*ca.* 1,200	...	...	...	1,200	...	...	1,700

EFFICIENCY AND CHOICE OF METHODS OF CLEARING AREAS. Different methods of removing drills to protect clams and efficiencies of these methods were compared during the afternoon low tide on June 26. Eight areas 3 feet (0.9 m.) square, 4 in plot 1 and 4 in plot 2, were chosen at random and marked out with stakes. Surfacing and humping drills in each area were picked up. Then 4 areas were raked with a garden rake with teeth 3 inches long and 1 inch apart. The other 4 were cultivated with a 5-tyne hand cultivator 10 inches (25 cm.) wide. All drills exposed by these treatments were removed and counted. Finally the upper 6 inches of soil from each area was sifted through quarter-inch mesh wire screen and the catch in each area counted. Results appear in Table II. In all, 45 drills were recovered from the 72 square feet of beach—an average of 0.6 drill per ft.^{2}.

The 4 picked, raked and screened areas yielded a total of 25 drills of which 3 (12%) were recovered by picking the surfacing and humping drills and 21 (84%) by picking and raking combined (Table II). The 4 picked, cultivated and screened areas yielded a total of 20 drills of which 1 (4%) was removed by picking and 12 (60%) by picking and cultivating combined.

Daylight picking of surfacing and humping drills is obviously not an efficient method of clearing (9% efficient, Table II). If it must be used, careful search should be made for humping drills because their numbers are on the average much greater than that of drills actually surfacing. This is not shown by Table II but it is clear from data for plots 2 to 4 in Table IV. Corresponding entries for whole plot or for stock area show that the numbers of drills surfacing composed only about 25% of those collected; i.e., surfacing and humping combined.

TABLE IV. Counts of drills in experimental plots after clam plantings. The initial population estimate, in the last line, is based on a raking efficiency of 84%.

Date and time	Plot 1 (Undisturbed)	Plot 2 (Planted only)				Plot 3 (Cleared and planted)				Plot 4 (Cleared, planted and picked thereafter)			
	Surfacing	Surfacing		Collected and replaced		Surfacing		Collected and replaced		Surfacing		Collected and destroyed	
	Whole plot	Whole plot	Stock area	Whole plot	Stock area	Whole plot	Stock area	Whole plot	Stock area	Whole plot	Stock area	Whole plot	Stock area
July 1–2, 2230–0200	...	...	...	...	...	...	...	...	106	...	...	912	...
July 2, 0900–1100	...	...	...	...	...	...	...	...	...	...	...	281	110
July 4–5, 2300–0200	...	...	...	...	179	340	...	...	178	...	...	1,253	267
July 6, 1330–1530	68	80	19	...	89	48	14	...	85	29	13	235	72
July 8, 0330–0500	536	628	81	...	152	301	38	...	68	285	62	412	99
July 11, 0500–0800	46	134	26	...	87	93	18	...	53	58	14	426	56
July 11, 1830–2000	33	45	22	...	91	33	15	...	51	...	...	...	...
July 12, 0645–0830	51	111	11	...	29	74	17	...	43	23	6	182	33
Average	147	200	32	...	105	148	20	...	83	89	24	529	106
Total	...	...	...	...	...	...	...	...	...	...	...	3,701	637
Estd. initial population	1,700	...	...	1,200	...	...	...	1,200	...	...	...	1,700	...

The low efficiency of picking only surfacing drills was demonstrated again from 0700 to 0830 hours on July 12 (not reported in tables) in two 10-foot-square areas in plot 3. Surface counts showed 1 snail in each area. No count was made of humping snails. By raking, one area yielded 41 more snails and the other 22. Correcting for efficiency of surface picking and raking combined (84%—Table II) the drill population of these 2 areas is estimated as 77. On this basis the 2 surfacing snails picked that day constituted only 3% of the total population. This agrees well, too, with the data gathered for plots 1 and 2 in the period June 27 to July 1 (Table III). These show that numbers of surfacing drills vary greatly, perhaps from hour to hour or with general meteorological conditions, and average 2 to 4% of estimated total populations.

The same data also illustrate the fact, well known to clam diggers, that more drills surface by night than by day. For instance, on June 29 between 1800 and 1930 hours (Table III) the number surfacing was 5 to 7% of the total population or roughly twice the 3% daytime value. On rare occasions, for example July 8 (Table IV), the night-emergence in plots 1 and 2 was as much as 10 times the normal day-emergence and 30 to 50% of the estimated total populations. Night picking would, therefore, be more efficient than day picking if areas to be cleared could be covered systematically.

For experimental work it appears that, where it can be applied, picking of surfacing and humping drills combined with cultivating (60% efficient) is a better method of clearing than picking alone, the efficiency of which varies greatly from time to time (av. 9%, Table II). Picking and raking combined (84% efficient) is still better. Screening is the best method and is considered 100% effective for the sizes of drills which populated these areas. But it is slow and laborious. The best method for preliminary clearing of the barren experimental plots seemed, therefore, to be a combination of picking and raking. But because raking is likely to damage small, shallow-burrowing clams (Medcof, 1950), picking, even though inefficient, seemed the only practicable method of clearing drills from plots after clams were planted in stock areas. Since night picking is more efficient than day it was decided to work during both day and night exposures of the flat whenever possible.

PRELIMINARY CLEARING. The experiment called for preliminary clearing of plots 3 and 4. This was carried out from June 28 to July 1 by picking, raking and destroying 1,036 drills from plot 3 and 1,432 from plot 4 (Table III). Correcting for 84% efficiency, total initial drill populations are estimated to have been 1,200 and 1,700 or about 0.5 per square foot. These estimates agree well with those for plots 1 and 2 based on screenings of small areas (Table II). They might be criticized however as likely too high because they are based on several rakings and pickings—not a single treatment which is 84% efficient.

CLAM PLANTING. Seed clams 1½ to 2 inches (38–51 mm.) long were dug from high levels on Pottery Bridge flat at St. Andrews during the evening tide on June 30, 1949. They were carefully culled to exclude all that were damaged and divided into lots for planting in stock areas and accessory plots as shown in

Table V at Holts Point during the morning tide July 1. Areas were scuffed to a depth of 4 or 5 inches with a hand cultivator before planting to make it easy for clams to work into the soil. To insure uniform stocking at 16 per ft.^{2} the plots were planted through a grid. This was made by stringing codline, at 3-inch (7.5 cm.) intervals, lengthwise and crosswise on a wooden frame 2 feet (0.6 m.) by 3 feet (1.0 m.). As in the 1948 and 1951 experiments, clams were pressed gently into the loosened soil, 1 to each grid square, so they stood vertically with siphon end uppermost and level with the surface. Examination of plantings at evening tide on July 1 indicated that for practical purposes there was no planting mortality.

TABLE V. Numbers of clams planted in various plots on July 1, 1949, and numbers and descriptions of clams and empty shells recovered on July 13–15, Holts point.

	Plot No.					Accessory plots		
	1	2	3	4	Total	Low	High	Total
Clams planted	0	1,476	1,476	1,476	4,428	576	444	1,020
Clams recovered	0	286	454	504	1,244	121	47	168
Not drilled	0	251	437	476	1,164	104	45	149
Drilled but not perforated	0	35	17	28	80	17	2	19
Survival	...	19%	31%	34%	...	21%	11%	...
Empty shells recovered	0	60	60	48	168	43	42	85
Not drilled	0	30	33	25	88	11	12	23
Drilled but not perforated	0	4	3	6	13	2	0	2
Drilled and perforated	0	26	24	17	67	30	30	60
Clams killed	0	1,190	1,022	972	3,184	455	397	852

POST-PLANTING OPERATIONS. In the 12 days following planting the plots were visited 8 times (Table IV). Surfacing and humping drills from plot 4 were removed and destroyed at each visit. Those in the other plots were merely collected, counted and replaced.

On July 13 the planted stock areas were dug with clam hoes and all living clams and empty shells were separately collected for each. They were twice re-examined, July 14 and 15, after the surface had smoothed off with wave action. A few clams were found, betrayed by their siphon holes, and a few empty drilled shells. Subsequent screenings of samples of the upper 8 inches of soil produced no more clams or shells. Presumably, all had been recovered. No live clams were found in the plots outside stock areas. All those missing are assumed to have been killed by drills.

The high and low undisturbed accessory plots (Fig. 1) were dug on July 14 and on July 15 and 16 they were given re-examination treatments like those for stock areas in plots 2 to 4. Results of all diggings appear in Table V.

SAMPLING DRILL POPULATION FOR SIZE-COMPOSITION. Two samples of drills were preserved to study size-composition of the population of plot 4. The first was a random sample of 420 from the night collection of July 4 to 5. The second was the whole of the day collection of July 6 (Table IV).

DISCUSSION

Manual Collection as a Means of Control

Preliminary clearing, June 28 to July 1, removed 1,432 drills (at least 84% of the total) from plot 4 (Table III). Most of the additional 3,701 collected from it, July 1 to 12, and destroyed (Table IV) are believed to have entered in the course of experiment (Table IV). The number that entered was undoubtedly greater than this, perhaps as great as 6,000, because the last collection was in daylight and yielded 182 surfacing and humping drills which probably represented about 9% of the plot's total population at that time (Table II). Thus, probably 300 and possibly as many as 500 drills were entering this plot every day of the experiment. Obviously drills can move about quite actively.

Surface counts of drills in plots 2 and 3 (Tables III and IV) show that drill populations suddenly increased 5 to 10 times following planting of their stock areas. Besides this, abundance in stock areas became higher and continued higher than in unplanted parts of plots. This shows that although drills can move quickly, they usually stay in an area once they find food there.

If the high count in plot 1 on the early morning of July 8 (536, Table IV) is neglected, it appears that there was little change in the drill population in this plot during the experiment. No clams were planted there and this result would be expected. If the drills moved into it they moved out just as quickly. There was nothing to attract or hold them there.

Clam survival was low in all plots (Table V). It averaged 16% in undisturbed accessory plots; 19% in plot 2 where there was no drill control, and 31% in plot 3 where drills were cleared before planting. In plot 4 laborious post-planting collection of surfacing and humping snails in addition to preliminary clearing effected no commensurate improvement—survival 34%.

It may be unjust to make direct plot-to-plot comparisons of survivals because there was a larger initial drill population in plot 4 and because proportionately more drills may have moved into it during experiment.

Results from plot 4 compared with those from plot 2 and accessory plots indicate that even picking and raking combined would not provide worthwhile protection for clam stocks in the Fundy region. Here clams require 4 to 6 years to reach commercial sizes. The 12 days' intense protection improved survival only from 16% to 34%. We must conclude that even if this full protection had been continued all planted Holts Point clams would have been killed in a few weeks if they had not been dug for purposes of experiment. This conclusion is supported by the results of the exploratory experiment. In the lowest of the 3 plots planted in the 1948 experiment 100% of the clams were actually destroyed.

Clearance of naturally-stocked areas by raking or cultivating appears impossible without serious damage to clam stocks. Collecting surfacing and humping drills, as practised in Massachusetts, seems to be the only available method of protecting public fishing areas. But at Holts Point, results would not justify

such efforts. This conclusion is at variance with that from the earliest drill studies, for example Belding's (1931), but is in accord with Turner's (1949, p. 5). Turner was not optimistic about coping with the droves of these hungry animals.

Clam Survival at Different Beach Levels

Comparison of survivals in the high accessory plot (11%), plot 2 (19%) and the low accessory plot (21%) suggests that drills were more active at high than at low beach levels. This contradicts our 1948 findings. From this we conclude that differences in beach level are less important in affecting drill distribution than other place-to-place differences which have not been investigated.

Feeding Habits

Table V reports numbers of empty shells recovered from stock areas. Many were buried but most were taken from the surface. From observing drills at work, it appeared that they burrowed deep to seize clams then worked their way up until they were close to or at the surface. Sometimes, especially at night, they surfaced and crawled about for considerable distances each carrying its victim in a temporary pouch in the foot which appears as a bustle-like hump just behind the shell spire. This pouch is formed by an infolding of the ventral surface of the posterior part of the foot. While the drill is crawling the clam is held so its long axis is parallel to the direction of the drill's progress.

Before they settled down to shell-drilling and feeding, most drills dug in again but not very deep. Occasionally at night they began feeding while still on the surface (Fig. 2). They left empty shells at or near the surface wherever they finished feeding. Here, shells are easily caught up by wave action and carried off. This accounts for the small number of shells (168) recovered from stock areas (Table V) relative to the number of clams killed (3,184) and for the drilled shells frequently observed at the edge of the shingle or on the flat far beyond plot borders.

Almost without exception the valves of recovered shells were still attached by their hinge ligaments, which made them convenient for study. Only 40% of paired valves were perforated by a drill hole, 8% showed beginnings of a drill hole but were not perforated, while 52% showed no drill mark whatever. An acceptable explanation is that about 60% of the time greater clam drills destroy soft-shell clams without perforating shells. The senior author has many times separated greater clam drills from bar clams (*Spisula*) on which they were feeding. In several instances the meat was nearly all gone but the shell intact. The ratio, number of drilled to number of undrilled dead shells in an area, has sometimes been used in judging the relative importance of drills in contributing to shellfish mortality. Our observations show that this can be misleading.

Table V shows that in plots 2, 3 and 4 and in accessory plots the number of living clams with shells drilled but not perforated was about 2% of the number killed. These clams may have been too large or too hard-shelled for drills to destroy.

A study of 50 of the 127 drilled shells recovered from all plots shows that perforations were seldom more than 10 mm. from the umbo. In 37 cases it was posterior and in 13 cases anterior, much as in samples Belding (1931) examined. There is obviously some selection of boring site in relation to the umbo.

The clam's normal stance in the soil is upside-down and Belding considered its posterior end as the first and easiest point of attack for any drill that might burrow down after it. However, in sandy soils, drills seem to have no difficulty in burrowing to depths of at least 8 inches, which is greater than the average depth of 2-inch clams (Medcof, 1950). Besides this, drills apparently do not drill their prey *in situ*. They bring it to the surface and drill and feed there at leisure. The fact that the posterior end of the clam is uppermost in the soil is probably unimportant in determining the common posterior position of drill holes in clam shells.

In the same sample of 50 shells referred to above, 31 were drilled in the left and 19 in the right valve. This distribution suggests preference for left valves but the evidence is weak.

Seemingly it is convenient for drills to hold clams in a particular position and to drill them at a particular place perhaps because of the shape of the clam's shell or of the drill's foot.

Size-Composition of the Drill Population

Fig. 3 describes size-composition of a day and a night collection of drills from plot 4. These were samples of humping and surfacing specimens picked by hand and might be criticized as not representative of the population. However, inspection revealed no obvious difference between these and lots obtained by screening or raking. Both curves in Fig. 3 would be unimodal with a little smoothing and it is the writers' opinion that several merged year-classes are represented in each collection. It is impossible to say why they should be so completely merged but differences in rate of growth of the two sexes could explain it. Direct observation showed that males in mating pairs were almost always smaller than females. This suggests different growth rates.

Turner (1951, p. 8) has offered a quite different explanation of unimodal size-composition in *P. duplicatus* although he too did not study sexes separately. He believes there is an abundance of food for juveniles but a scarcity of food for adults. Thus he belives that young drills grow rapidly and adults slowly and that this results in a telescoping of year-classes into a single size-class. This may or may not apply at Holts Point where drills regularly preyed on mussels of various sizes which are abundant close to plot 1.

It is not certain why modal size was smaller for the night (ca. 27 mm.) than for the day (ca. 30 mm.) sample. The junior author, who made most counts, believes that this difference is an error of the sampling. By day, most animals at the surface are inactive. The foot is withdrawn so that only the sand-coloured shell can show. Thus, smaller sizes may be easily overlooked and poorly represented in picked samples of drills. At night, on the other hand, surfacing drills

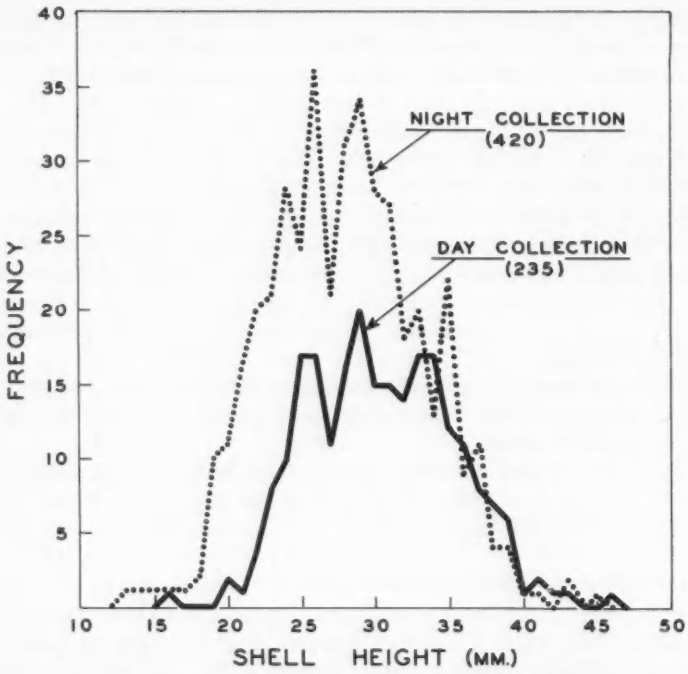

FIG. 3. Size-composition (shell heights) of midnight (July 4–5) and noonday (July 6) samples of surfacing and humping drills from plot 4.

are usually crawling about. The glossy white foot is extended and shows up conspicuously, regardless of its size, in the beam of a flashlight. There is, accordingly, less likelihood of overlooking small animals at night and this could account for the difference in modal sizes.

The largest drills were less than 50 mm. high (Fig. 3). In the southern Gulf of St. Lawrence, this species not infrequently attains 80 to 90 mm. Water is warmer there in summer and feeding and growing conditions may be better.

The smallest Holts Point drills were 13 mm. high (Fig. 3) and all small sizes were rare both in these picked collections and in samples screened from beach sand. Scarcity of small drills seems to be general in the Fundy area. It was observed by Dr. M. E. C. Giglioli for Belliveau Cove, Nova Scotia, in 1948. This peculiarity may have led early students to mistake the lesser clam drill, *L. triseriata,* which often occurs in the same areas, for the young of *L. heros.* In Massachusetts, Turner (1951) noted a similar scarcity of juveniles of *P. duplicatus* and believed it resulted from their rapid growth to modal size. Dr. J. L. Hart suggests that cannibalism might produce such a picture. We are unable to say which of these explanations is more likely. We expected to find an abundance of small drills somewhere.

If there were a nursery for young drills near by, removal of adults from the flat itself would not likely have any lasting effect on drill populations or clam survivals. The stock of juveniles in the nursery could be constantly maintained by settlements of pelagic larvae (Giglioli, 1955) which are borne great distances by tidal currents. This would provide unending supplies of young animals to migrate, perhaps as Shuster (1951) describes it, from the nursery onto the flat where drill control is attempted.

Results of this experiment show that manual collection of drills may improve survival of planted clams over short periods but cannot be considered an effective method of control. Giglioli's (1955) findings suggest that collection and destruction of the drill's egg masses is equally futile. The species is enormously fecund and its larvae are pelagic. Loosanoff (1956) is patiently testing various chemicals for attracting adult drills to traps. Effective and practical methods for control are badly needed in many areas.

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Determination of Natural and Fishing Mortalities of Cod and Haddock from Analysis of Tag Records off Western Nova Scotia[1,2]

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ABSTRACT

With marine species the population of tagged fish is unlikely to be a closed one, and previously described methods of determining natural and fishing mortalities are then hardly applicable. It is shown that when no data on effort or catch, related to tag returns, are available, a relationship between fishing and natural mortalities can be calculated, subject to some restrictive assumptions. An independent estimate of total mortality is then necessary to arrive at values of natural and fishing mortality.

The method is applied to taggings of cod and haddock off Nova Scotia (McCracken, 1956). For cod the calculations show wide variations in effort. We obtain a rather low value of the natural mortality in the first year of recoveries. In subsequent years the numbers of returns are so low that heavy losses of tags are suspected. For haddock the calculations show that the effort may be constant and that already developed methods (Leslie and Davies, Ketchen, DeLury, Beverton and Holt) may be applied. Results leave several alternative explanations possible, giving a range from 0 to .36 for the instantaneous natural mortality rate, depending on the unknown initial loss of tags.

INTRODUCTION

A TAGGING EXPERIMENT which provides data on recaptures over several fishing seasons (years) can be used to estimate fishing and natural mortalities, or at least their relationships. The methods applied so far (cf. Beverton and Holt, 1954, 1956; DeLury, 1958) have assumed a closed population and some additional information, such as data on effort or total catches. Especially with marine species, however, quite often the population of tagged fish may gradually spread over a larger (fishing) area than it originally occupied, and it becomes difficult to relate the tag returns to any figures on effort or total catches; or then there may not exist any data on effort or on total catches. The following analysis shows that even under these circumstances a relationship between fishing and natural mortalities may be obtained.

The method described will then be applied to taggings of cod and haddock off western Nova Scotia in 1953. These tagging experiments were planned by Dr. F. D. McCracken and carried out under his supervision (McCracken, 1956). Using records of recaptures from 1953–57 a relationship between instantaneous natural mortality rate and average total mortality rate is derived for both cod

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and haddock. These relationships are compared with independent estimates of the total mortality rate from age frequencies to obtain values of natural and fishing mortality rates.

The time distribution of tag returns of haddock, when corrected for the loss of tags due to fishing and natural causes, indicates that the fishing effort expended on the population of tagged haddock has been relatively constant. Assuming a constant effort, the modifications due to Beverton and Holt (1954) and Ketchen (1953) of methods originally developed by Leslie and Davies (1939) and DeLury (1947) have also been applied to haddock data. By assuming an initial loss of tags and letting it vary, a wide range of values, extending from 0 to 0.36, for the instantaneous natural mortality rate is obtained while the total mortality has a constant value. This total mortality obtained from tagging data is considerably higher than that obtained from age frequencies. The confidence limits for both of the estimates are so wide, however, that it cannot be ascertained whether this difference is genuine.

METHOD

The number of recaptures from a population of tagged fish reflects the effort expended on this population. The total number recaptured gives directly the rate of exploitation. Since the natural mortality and thus the number of tags in the water at any given time are not known, the information on the numbers recaptured cannot be converted directly to (instantaneous) fishing mortality rate. If, however, we assign arbitrarily, e.g. a constant value for the natural mortality rate, the fishing mortality rate corresponding to this assumed value can be calculated. By calculating the fishing mortality rate for several alternative natural mortality rates, a relationship between the two rates is obtained.

To be able to determine this relationship when the fishing effort and thus the numbers recaptured change with time, we divide the year into smaller time units within which the effort can be considered constant. All the calculations are then carried out separately for these smaller time units, and the resulting instantaneous rates are totalled to obtain the annual rates.

To derive the formulae used here we let N_v denote the population size of tagged fish at beginning of the v^{th} unit time interval (e.g. a month, a quarter) and let n_v, F_v and M_v be the number of returns, the instantaneous fishing mortality, and the instantaneous natural mortality, respectively, during the course of the v^{th} time interval. The time unit is assumed to be small enough so that F_v and M_v can be regarded as constants. We have

$$(1) \qquad n_v = \frac{F_v}{M_v+F_v} N_v(1-\exp-(F_v+M_v))$$

If the N_v is known, N_{v+1} can be obtained from the following recursive equation:

$$(2) \qquad N_{v+1} = N_v \exp-(F_v+M_v)$$

i.e. if N_1 (the number of fish tagged) is known, N_2 can be calculated from (2) after first solving for F_1 from equation (1) and so on for N_3, N_4, etc. If heavy, but unknown, initial losses of tags are suspected then the relationship between F and M must be calculated separately for different values of N_1.

Equation (1) cannot be solved explicitly but with reference to the table of corresponding values of, in our notation, $(F+M)$ and $(1-e^{-(F+M)})/(F+M)$ in Ricker (1948) approximate values of F can be obtained rapidly by iteration. We have, however, used an approximation which will also be given.

Approximate Solutions of Equations (1) and (2)

By expanding the exponential function $\exp-(F_v+M_v)$ as a power series, and by retaining only the terms of second order we get from (1):

$$n_v = F_v N_v \left(1-\frac{F_v+M_v}{2}\right)$$

This can also be written in the form:

$$F_v = \frac{n_v}{N_v} \div \left(1-\frac{F_v+M_v}{2}\right) \tag{3}$$

From (3) it is obvious, since $\frac{F_v+M_v}{2}$ is quite small, that n_v/N_v would differ but little from F_v. If we substitute $F_v = n_v/N_v$ in (3) we obtain:

$$F_v = \frac{n_v}{N_v} \div 1\left(-\frac{\frac{n_v}{N_v}+M_v}{2}\right) \tag{4}$$

This approximation has been found sufficient in all cases considered ($F_v+M_v \leqq 0.30$), giving the accuracy in general to the second decimal.

Modification of the Leslie and Davies Method

Because the modification of the Leslie and Davies method by Ketchen is not so well known and has not been used to estimate natural mortality, we will give a short account of it.

C_t denotes now the accumulated catch; N_t, the population at time t ($t \geqq 1$); f, the constant effort; and q, the ratio of F/f, (i.e. the fraction of the total population caught by one unit of effort), then we get as in (1):

$$C_t = \frac{F}{F+M} N_1(1-\exp-(F+M)t) \tag{5}$$

But $FN_1\exp-(F+M)_t = FN_t = qfN_t = f(qN_t)$ where $qN_t = (qN)_t$ is the catch per unit of effort at time t. Equation (5) may therefore be written as:

$$f(qN)_t = FN_1 - (F+M)C_t$$

Since f, the effort, is a relative term, it can be expressed in any units we wish. We may take $f=1$, so that $F=q$. This gives:

$$(6) \qquad (qN)_t = FN_1 - (F+M)C_t$$

By plotting the catch (per unit of effort) against accumulated catch we get a straight line (6) providing that natural and tagging mortality rates are constant. In practice the line is fitted by the least squares method. The intersection of the line with the axis of accumulated catch is the estimate of the total number of returns to be caught. If this estimate is N_E then from (6):

$$FN_1 = (F+M)N_E$$

Hence:

$$(7) \qquad \frac{N_E}{N_1} = \frac{F}{F+M}$$

where F+M is the slope of the fitted line. When N_1 (the number of fish tagged, or the estimated number of fish in the water at the beginning of the study period) is known, F can be calculated from (7). In fitting the line the weighting factors $1/N-C(t)$, where N is a crude estimate of N_E, were applied (cf. Zippin).

EXAMPLES

In the summer of 1953, 1,800 cod and 580 haddock were tagged off western Nova Scotia (off Lockeport). From those fish, about 800 cod and 150 haddock were recaptured in 1953 to 1957.

Four types of tags—hydrostatic, Petersen red and white disks, Petersen yellow disks, and strap tags—were used. In general, the disk types of tag gave almost the same percentage recoveries, while the percentage recoveries for hydrostatic and strap tags were lower than those of Petersen disks (McCracken, 1956). The difference between hydrostatic and disk tags was great enough to be significant for cod but not necessarily for haddock. The percentage recoveries of strap tags were so low compared with the other tags that we have not used them in the analysis.

Cod

As the first application of the type of analysis proposed, we consider the cod tagging. The percentage recoveries of cod were in general quite high. In Table I the number of fish tagged, the numbers recovered in 1953, 1954, 1955 and 1956, along with the estimated numbers left in the water on the 1st of November 1953, are recorded for each type of tag. The last figures are obtained by discarding the returns before November and assuming alternatively 0.05, 0.16 and 0.29 instantaneous natural mortality rates. The monthly recoveries from November 1953 to October 1954 are given in the fifth column of Table II for

TABLE I. Tags applied to cod during the summer of 1953, off Lockeport, Nova Scotia, and the computed number left in the water on November 1, 1953, assuming three different natural mortality rates (M).

Type of tag	Number tagged	Number of returns in 1953	1954	1955	1956	Number of returns from Nov. 1, 1953 to Oct. 30, 1954
Hydrostatic	932	206	148	12	8	176
Disk	605	229	91	4	1	148
Strap	263					48

CALCULATED NUMBER OF TAGS LEFT IN THE WATER, NOV. 1, 1953.

	M = 0.05	M = 0.16	M = 0.29
Hydrostatic	765	748	712
Disk	434	411	396
Strap	240	237	230

disk tags. The number of returns reflects the effort expended on the tagged population. The total effort over the whole area does not follow the same pattern.

A month has been selected as a unit time interval. Using the formulae (2) and (4) successively, Table II is constructed for disk tags. Corresponding to each hypothetical natural mortality rate the table gives the estimated population size at the beginning of each month and the instantaneous fishing mortality rates during each month. The monthly instantaneous fishing mortality rates are then summarized to give the total instantaneous rate. The results including the

TABLE II. Calculated numbers of disk tags remaining on cod at the start of successive months (columns 2–4), number of returns during each month (column 5), calculated natural loss (columns 6–8) and calculated rates of fishing mortality, F (columns 9–11), for three different estimates of natural mortality (M).

1	2	3	4	5	6	7	8	9	10	11
	Calculated number of tagged fish			No. of returns	Loss for natural mortality			Estimated fishing mortality		
M →	0.05	0.16	0.29		0.05	0.16	0.29	0.05	0.16	0.29
1953										
November	434	416	396	24	2	5	8	0.057	0.060	0.063
December	408	386	362	14	2	5	7	0.035	0.037	0.040
1954										
January	392	367	339	7	2	5	7	0.018	0.019	0.021
February	383	355	324	7	2	4	7	0.018	0.020	0.022
March	374	343	309	6	2	4	6	0.016	0.018	0.020
April	366	332	296	9	2	4	6	0.025	0.028	0.031
May	355	319	280	36	1	4	6	0.107	0.120	0.139
June	318	279	237	35	1	3	5	0.117	0.135	0.162
July	282	240	196	20	1	3	4	0.074	0.088	0.109
August	261	217	171	9	1	3	4	0.035	0.043	0.055
September	251	205	158	9	1	2	3	0.037	0.045	0.059
October	241	193	145	0	1	2	3	0	0	0
December	241	186	154	...	...	...	...	...	...	...
Total instantaneous fishing mortality rate								0.539	0.613	0.721

two additional relationships, the one representing the hydrostatic tags and the other representing disk and hydrostatic tags combined, are plotted in Fig. 1.

The two types of tags give strikingly different results. For instance, at the total instantaneous mortality rate 0.60 the corresponding natural mortalities for hydrostatic and disk tags 0.32 and 0.07 respectively. The higher estimated natural mortality for hydrostatic tags is probably attributable to the higher tagging mortality or direct loss of tags. The results of other cod taggings in our waters exhibit the same phenomenon.

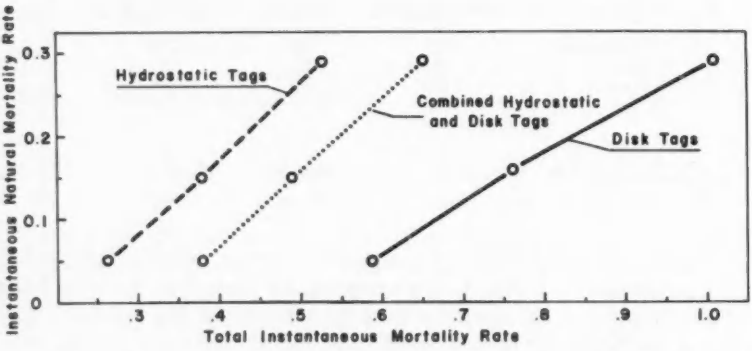

FIG. 1. Cod. Relation between instantaneous natural and total mortality rates based on 1953 Lockeport tagging.

The total instantaneous mortality rate for the Lockeport cod population is estimated from age frequencies to be about 0.60 (45%) for the summer seasons. From Fig. 1 we get a value 0.07 for the instantaneous natural mortality rate for disk tags (0.24 for hydrostatic and disk tags combined). The corresponding instantaneous fishing mortality rate is 0.53.

There are no confidence limits available for the total instantaneous mortality rate of 0.60. If we place them completely arbitrarily at 0.43, 0.80 (35%, 55%), which are quite high, then the corresponding values for instantaneous natural mortality rates are 0, .20 (0%, 18%).

Using the estimate 0.07 for the natural mortality rate, the fishing mortality rate (effort) can be obtained following the pattern of Table II. The values are plotted in Fig. 2. The fishing mortality is high during the months of May–August and comparatively low during the rest of the year. While the total catch is rather steady over the year, it indicates that the fishery must be concentrated on at least two semi-discrete populations; we may call them the summer and winter populations. During the winter, fishermen move to deeper water where the population is only partly mixed with the population fished during the summer.

In the second year after the tagging (i.e. in 1955) the number of recaptures dropped considerably. By using the rate M=0.07 together with the known fishing mortality, the number of tags in the water at the beginning of the years

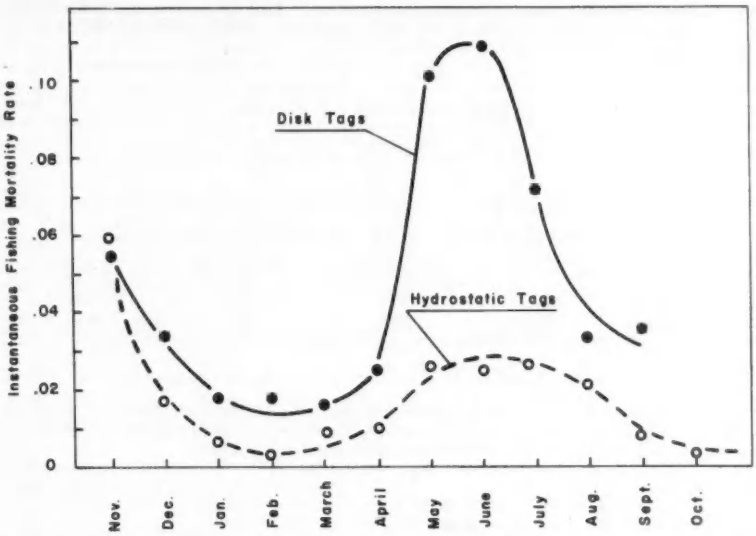

FIG. 2. Cod. The distribution of effort expended on the summer populations as estimated from tag returns.

1954 and 1955 can be estimated. In 1954 about 38% of the estimated number of disk tags in the water at the beginning of the year were recovered, in 1955 only 5% were recovered. This phenomenon is associated both with the almost complete absence of older cod (8–9 years old) in age frequencies and with the loss of tags due to growth (McCracken, personal communication). On that account no further calculations have been done. It is quite obvious, however, that without further study the low natural mortality rate obtained for one year can hardly be generalized.

HADDOCK

All haddock were tagged in the vicinity of Lockeport, N.S. From the total number of returns in 1954, about 54% of the tags came from the inshore grounds close to the tagging area, 42% came from the adjacent LaHave and Browns Banks, and 2% from more remote grounds. In general, the movement took place in an easterly direction along the shore or to the nearby offshore banks.

In contrast to cod, haddock tag returns did not exhibit any unusually high percentage recoveries during and immediately after the tagging period. This may be attributable to the fact that haddock move around more, mixing rapidly with the rest of the population. In relation to the fishing areas the fishery exhibits a pronounced seasonal pattern. Because of this and the fact that the numbers of tagged fish present at any one bank are not known, we cannot relate any effort or catch figures to tag returns.

TABLE III. Tags applied to haddock during the summer of 1953, off Lockeport, Nova Scotia, and the computed number left in the water on November 1, 1953, assuming different natural mortality rates (M).

Type of tag	Number tagged	Number of returns in 1953	1954	1955	1956	1957
Hydrostatic	276	14	31	18	7	5
Disk	185	13	27	18	8	8
Strap	119	...	...	...	...	...

CALCULATED NUMBER OF TAGS LEFT IN THE WATER, NOV. 1, 1953.

	M = 0.20	M = 0.30	M = 0.40	M = 0.50
Hydrostatic	248	241	233	224
Disk	163	158	152	148

TABLE IV. Estimates of quarterly fishing mortality rate, F, for haddock, from combined returns of hydrostatic and disk tags, using the procedure of Table II. Roman numerals refer to 3-month seasons, starting with I = February, March and April.

1	2	3	4	5	6	7	8	9	10
Season	Calculated number of tagged fish surviving				No. of returns	Fishing mortality, F			
M →	0.2	0.3	0.4	0.5		0.2	0.3	0.4	0.5
1953									
IV	411	399	385	372	14	.036	.037	.039	.041
1954									
I	377	357	335	315	26	.073	.079	.085	.092
II	333	306	278	253	13	.041	.045	.050	.056
III	304	272	239	211	11	.038	.043	.050	.057
IV	278	243	206	176	5	.019	.022	.026	.031
1955									
I	259	221	182	151	21	.087	.104	.129	.160
II	226	185	145	114	8	.037	.046	.060	.078
III	207	164	124	93	3	.015	.019	.026	.035
IV	194	149	110	79	4	.021	.028	.039	.056
1956									
I	181	134	97	66	6	.035	.048	.067	.102
II	166	119	82	53	1	.006	.009	.013	.020
III	157	109	73	46	4	.026	.039	.059	.097
IV	146	97	62	37	7	.050	.078	.126	.224
1957									
I	132	83	49	26	3	.024	.038	.067	.131
II	123	74	41	20	4	.034	.058	.108	.239
III	113	65	33	14	3	.028	.049	.101	.258
IV	105	57	27	10	0	0	0	0	0

We will assume, quite arbitrarily, that the natural mortality rate is constant and the same for all areas. We also consider the case when there have been heavy initial losses of tags by letting the initial number of tags vary over a wide range.

In Table III the number of fish tagged by type of tag, the number of hydrostatic and disk tags recovered, and the estimated number of hydrostatic and

TABLE V. Yearly total instantaneous fishing mortality rates, F, from Table IV, and 4-year averages for F and for instantaneous total mortality rate, F+M. N_1 is the computed initial number of tags in the water on November 1, 1953.

	Fishing mortalities (F) for the year			
	M = 0.20	M = 0.30	M = 0.40	M = 0.50
N_1	411	399	385	372
1954	0.171	0.189	0.211	0.236
1955	0.160	0.197	0.254	0.329
1956	0.117	0.174	0.265	0.443
1957	0.086	0.145	0.276	0.628
Av. F	0.133	0.176	0.252	0.409
Av. F+M	0.333	0.476	0.652	0.909

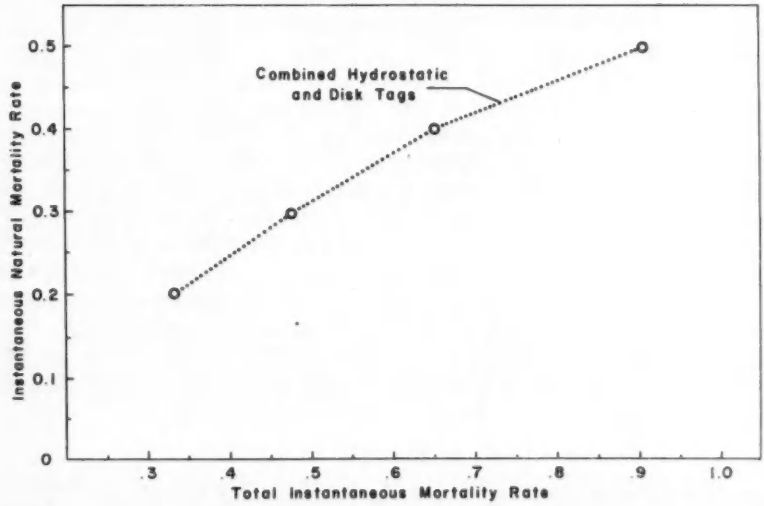

FIG. 3. Haddock. Relation between instantaneous natural and total mortality rates based on 1953 Lockeport tagging.

disk tags left in the water on the 1st of November 1953, are given. In estimating the numbers left in the water 0.20, 0.30, 0.40 and 0.50, instantaneous natural mortality rates are assumed. Table IV, the sixth column, gives the number of recoveries of hydrostatic and disk tags combined, by seasons. It also gives the estimated population sizes at the beginning of each season and the instantaneous fishing mortality rates during each season corresponding to four different instantanteous natural mortality rates. Table IV is summarized in Table V and in Fig. 3.

In Table VI we have summarized the situation for M=0.16, 0.24, and 0.30 when an initial loss of about 210 tags is assumed, leaving 250 tags in the water

on November 1, 1953. This figure was selected quite arbitrarily just to see whether the results agree with the independent estimate of total mortality from age frequency.

TABLE VI. Yearly total instantaneous fishing mortality rates etc., calculated as in Table V but with the additional assumption that there is an initial loss of about 210 tags, leaving 250 tags in the water on November 1, 1953.

	Fishing mortalities by year		
	M = 0.16	M = 0.24	M = 0.30
N_1	250	250	250
1954	0.297	0.314	0.330
1955	0.304	0.362	0.418
1956	0.243	0.344	0.477
1957	0.191	0.329	0.562
Av. F	0.259	0.337	0.447
Av. F+M	0.419	0.677	0.747

There have been no big changes in the total fishing effort from 1953–57. However, if we assume the instantaneous natural mortality rate M=0.20, then, in the absence of heavy initial losses of tags, the fishing mortality rate decreases from F=0.17 in 1954 to F=0.09 in 1957 (Table V); at the rate M=0.40, it increases from F=0.21 to F=0.28. Providing that there has been no increase in the tagging or natural mortality and providing that the effort and the availability of fish have been more or less constant, the instantaneous natural mortality rate is apparently between M=0.20 and M=0.40, the instantaneous average fishing mortality being between F=0.13 and F=0.25. If we assume an initial loss of tags so that N=250 on November 1, 1953, then we get similarly the range of values from M=0.16, F=0.26 to M=0.30, F=0.45 (Table VI).

COMPARISON OF RESULTS WITH INDEPENDENT ESTIMATES OF MORTALITY RATES

Since our calculations do not refute the assumption that F is constant, we may apply the modification of the Leslie and Davis method by Ketchen to the data. This gives F+M=0.56[3,4] with the 95% confidence interval of 0.36 to 0.76. These limits are of course subject to the restriction that F and M are constant.

From age frequency data the value of F+M around 0.40 is obtained. This value combines in itself the variations due to changes in year-class strengths, changes in effort, and errors due to sampling, etc., and it should be regarded as rather unreliable. If, however, the difference between the total mortality estimates 0.40 and 0.56 is real, it suggests a continuing heavy (instantaneous) mortality

[3]We have used $1/200-C(t)$ as weighting factors. N_E is actually 144, rather than 200.

[4]If the Beverton and Holt method (cf. Beverton, 1954, pp. 137–139) is applied to the data, the same value of F + M is obtained. The 95% confidence interval is 0.81, 0.31. This method is, incidentally, a modification of the method originally given by DeLury (1947, 1954).

rate attributable to tagging. Such mortality, in the opinion of Dr. McCracken, is rather unlikely several years after the tagging.

When we do not assume any initial losses of tags, the value F+M=0.40 can be compared with results tabulated in Tables IV and V and in Fig. 3. The comparison suggests 0.40 is too low a value. If we assume a heavy initial loss of tags so that N_1=250, say, (i.e. that 250 tags are left in the water on November 1, 1953) then for M=0.16 we get an average F=0.26 with F+M=0.42. This is quite close to 0.40. However, it is seen from Table VI that the fishing mortality decreases now from 0.30 to 0.19 over the period from 1954 to 1957. There is no further information to support this but, of course, it is not entirely impossible.

Values of F and M, corresponding to F+M=0.56, obtained from tagging data can be calculated for different values of N_1 (cf. equation (7)). Thus for N_1=390 we get F=0.20 and M=0.36. Incidentally, this value of N_1 corresponds to the case when we have no initial loss of tags, other than due to the natural mortality M=0.36 (cf. Table IV). If we assume so high an initial loss of tags that only 144 fish are left on November 1, 1953, we get F=0.56 and M=0. If we calculate F year by year, for M=0, as in Table IV, it stays relatively constant over the period from 1954 to 1957. This is true for any other combinations of F and M for N_1 between 144 and 390. The implication of this is that we are justified in using the modification of Leslie and Davies' method by Ketchen and that, on the basis of tagging data, we cannot single out any specific value of M between M=0 and M=0.36.

ACKNOWLEDGMENTS

The data for the analysis were given by Dr. F. D. McCracken who was in charge of the tagging program. His views and his knowledge of the fishery have helped greatly in choosing the type of analysis employed. I also wish to thank Drs. W. E. Ricker and L. M. Dickie for their comments.

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Studies of Reproduction and Feeding of Atlantic Cod (*Gadus callarias* L.) in the Southwestern Gulf of St. Lawrenec[1]

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ABSTRACT

Size at maturity, time of spawning, fecundity and food of cod were examined in the southwestern Gulf of St. Lawrence during the summers of 1955 and 1956. In 1955 and 1956 males were 50% mature at 50 and 53 cm., respectively; females, for the same years, were 50% mature at 52 and 57 cm., respectively. The spawning period lasted from May to September, with peak spawning at the end of June. A cod of 51 cm. in length produced 200,000 eggs, while a larger specimen of 140 cm. in length carried 12 million ripening eggs.

Small cod, of 11 to 30 cm. in length, selected a diet of pelagic crustaceans, namely mysids, euphausids and amphipods. With increase in size, cod adopted a more varied diet, in which fish and benthic invertebrates became increasingly important. At lengths over 70 cm., pelagic and bottom forms were taken in approximately equal volumes. Herring was the most important fish in the diet of large cod over 50 cm. in length.

INTRODUCTION

During the course of tagging operations from a small research vessel in 1955, and during studies of fish discarded at sea from commercial draggers in 1956, the reproduction and feeding of 1,874 Atlantic cod were examined in the Bay of Chaleur area of the southwestern Gulf of St. Lawrence. These studies represent contributions to an intensive investigation of the effects of changes in the environment and fishing on the abundance and landings of cod along the Canadian Atlantic mainland.

Corbeil (1954b) studied cod food, and Jean (1954a) examined the spawning of cod in the same area. The present study contributes comparable data for later years, and it adds new information on size at maturity, fecundity, and food of small cod.

METHODS AND MATERIALS

Field work was carried out in the summers of 1955 and 1956 from the end of May to the beginning of September. In 1955 most of the cod were hand-lined during tagging operations from the Fisheries Research Board's 57-foot vessel *Mallotus*. Some fish were obtained from catches of the Board's 65-foot vessel *J. J. Cowie*, which was engaged in mesh selection work, using a ¾ #35 Yankee trawl with a small mesh cover. In 1956 the cod used in this study were sampled from catches of commercial draggers fishing out of Caraquet and Shippegan, N.B. Most of these boats used a #35 Yankee otter trawl, but some used a small ¾ #35 net. The areas of sampling are shown in Fig. 1.

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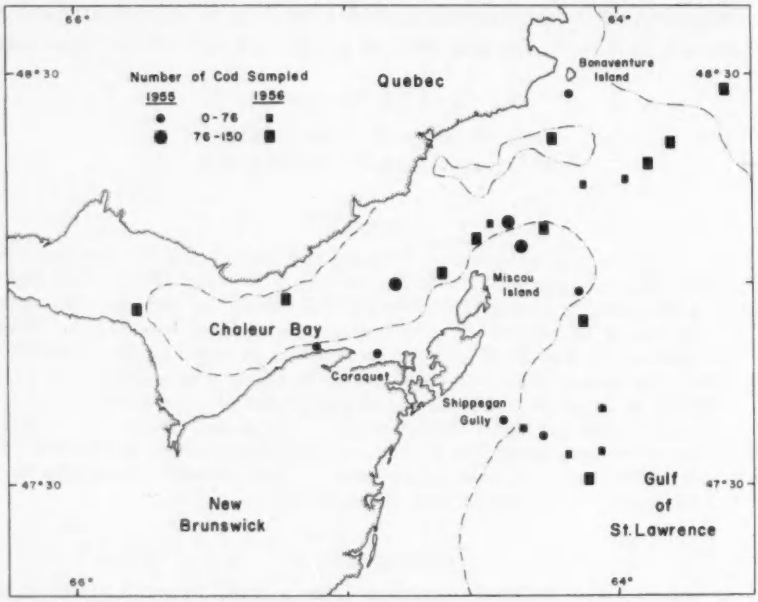

FIG. 1. Map showing distribution of cod samples taken in the southwestern Gulf of St. Lawrence in 1955 and 1956.

Gross examination of specimens was made in the fresh condition. For each fish the following information was recorded:

The length was taken as the distance between the tip of the snout and the tip of the shortest ray in the centre of the caudal fin.

Sex was recorded as male or female.

The gonads were classified as immature, ripening, ripe, spawning, spent, and recovering. Ovaries from 53 ripening females were preserved for fecundity studies.

Gross stomach analyses were made on 600 cod, while 620 cod stomachs were preserved for later detailed analysis in the laboratory.

Otoliths were taken from all fish used in fecundity studies, and from one tenth of those used in the gross analyses.

REPRODUCTION

The reproductive stages used in the maturity studies were similar to those employed by Hickling (1935) and Graham (1924). The full reproductive cycle was divided into 6 stages as shown in Table I.

SIZE AND AGE AT MATURITY

As part of the study of the biology of cod in the Bay of Chaleur area of the Gulf of St. Lawrence, the length at which 50% of the fish reached maturity was

TABLE I. Definitions of the sexual stages of cod used in the present study.

FEMALE	MALE
IMMATURE	
Ovaries pale pink, orangy, occasionally grey. In small fish membrane is thin and transparent, the ovary slack. In larger fish the membrane is thicker, the ovary more translucent and firmer.	Slender, knobbed, string-like organ. Pinkish in colour without coils or lobes.
RIPENING	
Ovary swollen to twice its former length and diameter. Small white opaque eggs numerous and visible to the naked eye, with surface of ovary permeated by small blood vessels. Ovary usually an opaque mass, but sometimes pink or even orange, depending on feeding habits during egg development.	Pinkish to white coloration and increase in volume. Texture pasty, firm and distended with fine, wavy blood vessels. When compressed no milt is expressed.
RIPE	
Ovary trebled in volume. Individual eggs now larger, discrete, and either transparent or with clusters of transparent eggs within the generally opaque mass of the ovary. Blood vessels less conspicuous. Pressure on ovary causes extrusion of a few eggs.	White and distended into wavy lobules. A small amount of milt may be forced out by pressure.
SPAWNING	
Transparent to pink-purplish in colour. Large transparent eggs expressed freely by exertion of pressure on jelly-like mass of the ovary.	Densely white and fully distended. Milt runs freely at the touch.
SPENT	
Eggs nearly all released, ovary purple in colour and flaccid. Membrane starts to thicken and shrink, leaving surface whitish with purple showing through.	Testes shrunken and reddish, lying loose in the body cavity. Vas deferens prominent against irregular surface of the organ.
RECOVERING	
Ovary beginning to take on pink or orange hue again in contrast to purple of the above condition. In smaller fish can be confused with immature condition, but membrane thicker and ovary firm.	Resumes a pale pink colour, somewhat similar to immature condition but larger.

determined. The percentage of mature cod in each 3 cm. length group is shown for the years 1955 and 1956 in Fig. 2. In both years the males attained the 50% mature point at a somewhat shorter length than the females.

In 1955 the length at which 50% of the males were mature was 53 cm., compared with 57 cm. in the females. In 1956 that length was 50 cm. in the males and 52 cm. in the females. Otoliths collected during the 2 years showed that these lengths corresponded to ages 4 and 5 years, and that no cod attained maturity before the 4th year.

The length at which 50% of the cod matured differed in the 2 years. It is thought that food may have had an important bearing on this difference, and this will be considered later under the section on food.

Maturity was attained at a shorter length and younger age than for cod in Greenland and Newfoundland waters. In Greenland waters as cod reach a length of from 70 to 80 cm. and an age of from 6 to 9 years, the majority spawn

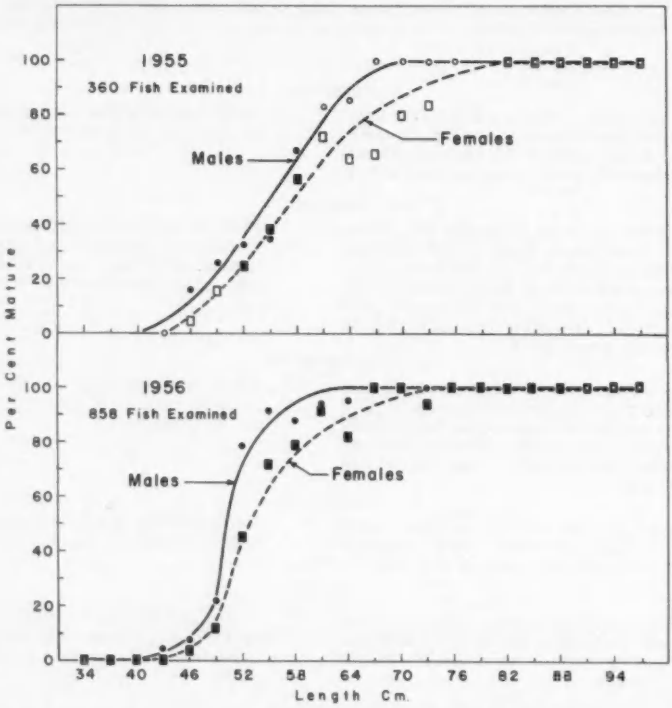

FIG. 2. Size at maturity of cod from the southwestern Gulf of St. Lawrence. Points plotted are mean values for each 3 cm. length group. Solid symbols represent 10 or more fish, and open symbols signify less than 10 fish.

for the first time (Hansen, 1949). In the Newfoundland area male cod first mature between lengths of 60 and 70 cm. and female cod at about 80 cm. In this area only 2% of cod attain first maturity at 4 years (Thompson, 1943).

In the Gulf of Maine cod attain maturity in their 3rd and 4th years (Bigelow and Schroeder, 1953). The cod in the southwestern Gulf of St. Lawrence seem to be intermediate in position between Newfoundland and Gulf of Maine fish, with regard to their age at maturity.

SPAWNING

Ripe and spawning fish were found in all localities sampled, but never in proportions great enough to show localized spawning grounds. Spawning appeared to take place over the whole area.

The time of spawning was determined by observing the percentages of each maturity stage throughout the 2 summers (Fig. 3, 4). Immature fish are not included in the graphs. Although the number of fish sampled in 1955 was not as large as for 1956, the results indicate a similar pattern for both years. The peaks of spawning occurred during the period June 17–30.

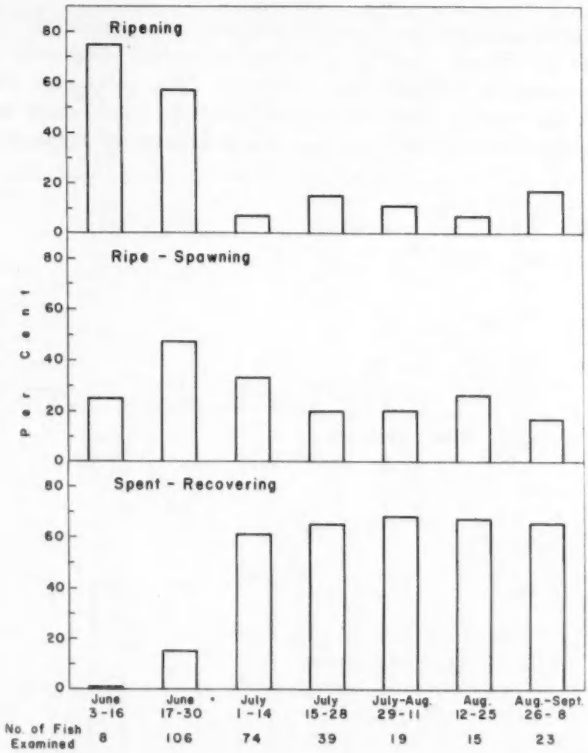

FIG. 3. Percentages of 3 main phases in the cod reproductive cycle from June to September, 1955, southwestern Gulf of St. Lawrence.

Jean (1954a) studied the variation in diameter of cod eggs from the same area for the period May 27 to October 2, 1953. The percentages of those sizes of eggs which corresponded to the ripe and spawning stages of maturity reached a peak from June 17 to July 2. Although the present study was carried out by gross analysis, it can be seen that there is good agreement from both studies as to when the peak of spawning occurs. It should be noted that spawning does not take place in a short period, but rather is spread out from at least May to September, the period during which observations were made.

FECUNDITY

Egg production was investigated in relation to two factors, length and age. While a third factor would have been desirable, that of weight, it was not available. During the course of the present work counts were made on opaque eggs in the ovaries of 53 ripening cod. These cod ranged in length from 51 to 140 cm., and represented cod of ages 4 to 17 years.

The ovaries selected for fecundity studies were preserved and fixed in formalin and in Gilson's fluid. A gravimetric method originated by Simpson (1951) was used to estimate the fecundity. The procedure differed from Simpson's in one respect. After the ovaries had been fixed, water was added to dilute the fixing solution, which became cloudy because of suspended fragments

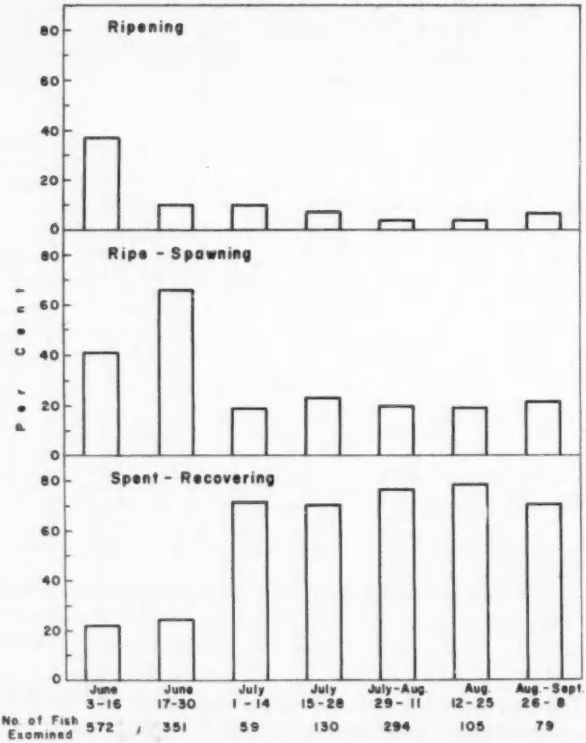

FIG. 4. Percentages of 3 main phases in the cod reproductive cycle from June to September, 1956, southwestern Gulf of St. Lawrence.

of ovarian tissue, the small eggs of subsequent years and bits of detached chorions. Initially, this fluid was decanted off the large, present-year eggs, but later quicker results were accomplished by washing the eggs through sieves of the type employed in entomological work. The sieves were 8 inches in diameter with brass frames. The mesh sizes used were #10, #20, and #70, which allowed the minute eggs of subsequent years to pass through and retained the present year's eggs.

The rest of the procedure involved the transference of the eggs to trays of blotting paper where they were dried slowly in front of a slow fan. On drying, the eggs turned various shades of yellow and brown and became very hard.

The same method was used for the eggs preserved in formalin. However, in these cases the ovarian tissue was not dissolved as it was in the case of the ovaries preserved in Gilson's fluid, and it was necessary to scrape the eggs off

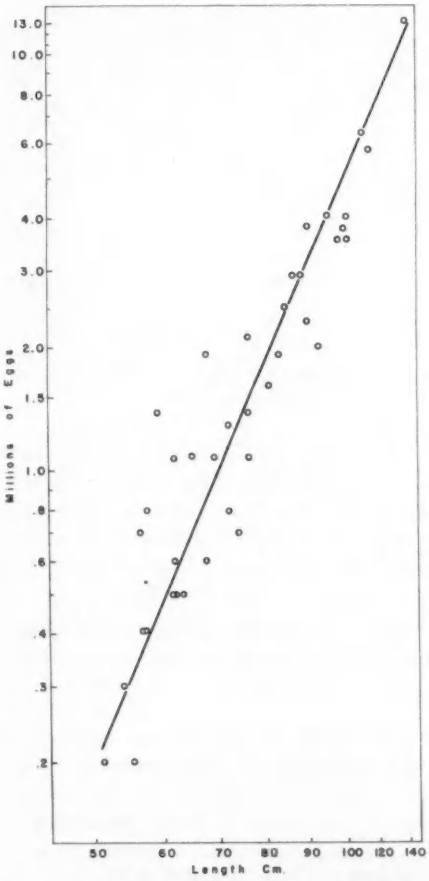

FIG. 5. Relationship between fecundity and length of cod in the southwestern Gulf of St. Lawrence. Points represent individual fish.

the walls of the ovary, and to separate out the connective tissue and lamellae. It was a very tedious process, but the eggs were found to dry satisfactorily.

The number of eggs from each cod was estimated by weighing the total number of dried eggs and then counting 3 samples of 500 eggs and weighing

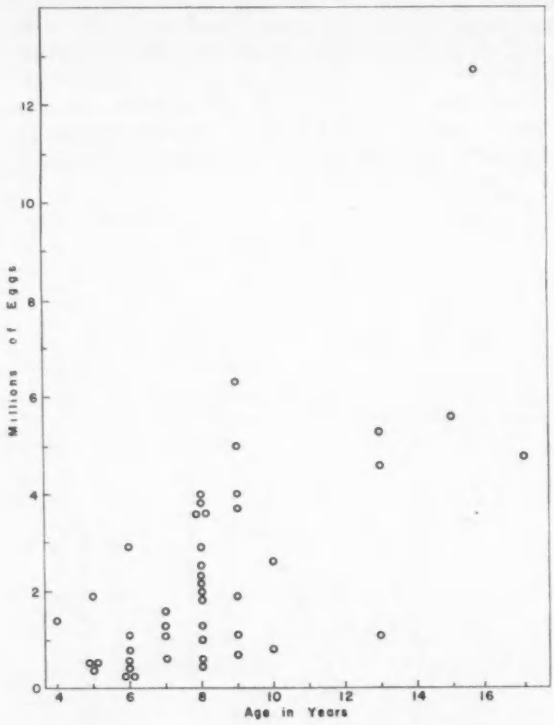

FIG. 6. Variation in fecundity among cod of certain ages taken from the southwestern Gulf of St. Lawrence.

these. The average weight of the 3 samples was used to determine the total number of eggs. A sample calculation is given below:

Weight of 500 eggs	Sample #1, 23.8 mg.; #2, 23.2 mg.; #3, 23.2 mg.
Mean weight of 500 eggs	= 23.4 mg.
Standard deviation	= 0.35
Standard error of mean	$= \frac{0.35}{\sqrt{3}} = 0.20$
95% confidence limits for mean	= 23.4±0.86
Total weight of eggs	= 34.434 gm.
Total number of eggs	$= \frac{34.434}{23.4} \times 500 = 735{,}000$
Range of eggs for 95% confidence limits	= 735,000±36,700

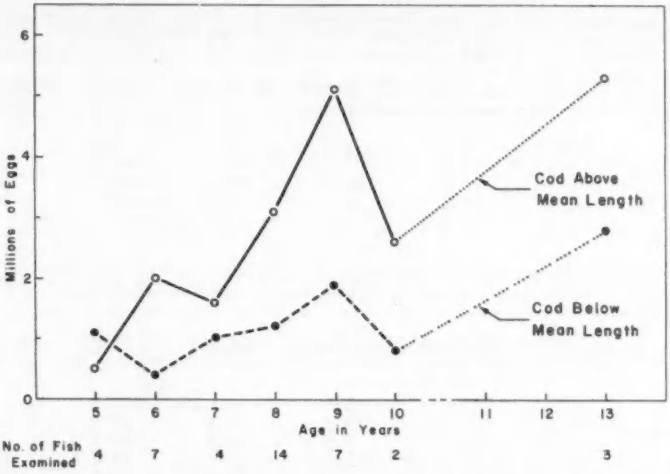

FIG. 7. Mean fecundities of cod shorter and longer than mean length in each age group.

The counts were plotted logarithmically against fish lengths (Fig. 5). The number of eggs increased rapidly with increasing size of cod, from 200 thousand in a 51 cm. cod to 12 million in the case of a cod 140 cm. in length.

There was considerable variation in the numbers of eggs in fish of the same age groups (Fig. 6). The variation in size within one age group was considerable, and since length probably exerts the stronger influence, its effect was then tested on the number of eggs by plotting the mean fecundity of those fish above and below the mean length of an age group. The mean fecundity was found to be greater in the longer or faster-growing fish (Fig. 7).

FOOD

During the study of feeding habits of the cod in the southwestern Gulf of St. Lawrence, 620 stomachs were examined in detail. In 1955, 289 stomachs were analysed, and the occurrence of each organism was recorded. In 1956, 331 stomachs were analysed, and the volume of each organism was recorded, as well as its frequency of occurrence. A total of 9 phyla and over 60 families were identified during the course of the study. Wherever possible, organisms were identified to species (Tables II, III).

Although the fish in 1955 were taken by a different method of capture (by handline) from those in 1956, there appeared to be no significant difference in the variety of food eaten in the two groups. However, annelids, crustaceans, fish, and molluscs were all found in greater amounts in 1956. It is also noted that the percentage of empty stomachs was lower in 1956 (6%) than in 1955 (15%).

TABLE II. The percentage of cod stomachs which contained each item of food in 4 length groups, 1955. Samples from all areas are combined, with empty stomachs included.

Length	Number of stomachs	Annelids	Echinoderms	Crustaceans	Fish	Molluscs
cm.						
11-30	23	4.3	4.3	91.6	8.6	6.0
31-50	70	15.5	7.1	83.9	17.2	22.7
51-70	79	21.7	20.0	76.3	39.4	30.2
71-90	38	3.5	17.8	75.0	57.1	17.8

TABLE III. The percentage of cod stomachs which contained each item of food in 5 length groups, 1956. Samples from all areas are combined, with empty stomachs included.

Length	No. of stomachs	Annelids	Echinoderms	Crustaceans	Fish	Molluscs
cm.						
11-30	94	10.4	1.5	96.5	8.9	2.2
31-50	94	21.2	10.6	89.3	29.7	15.9
51-70	84	28.8	7.9	81.4	52.2	35.3
71-90	44	37.1	8.7	69.2	61.2	45.0
91-120	15	16.6	8.3	75.0	66.6	33.3

FOOD HABITS OF COD IN RELATION TO SIZE

COD 11 TO 30 CM. LONG. Corbeil (1953, 1954b) carried out a commendable study of cod food in this region, with emphasis on fish of marketable sizes. The present study adds to that picture by including an analysis of stomachs from small cod, between 11 and 30 cm. in length.

Fig. 8 shows a volumetric analysis of the stomachs of 94 small cod. These fish were divided arbitrarily into two 10 cm. length groups.

The greater part of the diet of these small cod was made up of small crustaceans. Those fish of the 11 to 20 cm. group fed predominantly on mysids, euphausids, and amphipods. Certain species of crustaceans were very abundant. *Mysis mixta* and non-identified immature mysids were common and appeared even in the smallest stomachs examined. Euphausids, *Thysanoessa raschii* and *T. inermis*, were also found in great numbers, but it would appear that the larger size of the latter species prevents cod smaller than 16 cm. from taking them. Minute amphipods, especially *Hyperia* and *Euthemisto* spp. were present in the smallest cod examined. Small *Crago* and other decapod shrimps appeared first in cod of 15 cm., but were not abundant.

Since larger cod are mainly piscivorous, it is of interest to find out at which size this behaviour is first manifest. The smallest cod taken during the present study was 11 cm. in length. Very few cod between the lengths of 11 and 15 cm. were captured, but more were obtained between the lengths of 16 and 20 cm. Most of these contained small crustaceans. Of the 26 stomachs examined, only one, from a 19 cm. specimen contained fish. No cod smaller than 19 cm. contained fish.

Some forms, namely chaetognaths, caprellids and cumaceans were rarely present in the stomachs of cod below 20 cm. in length. The stomachs of 2 of 26

cod examined contained great numbers of partially digested arrow worms. Copepods of the family Calanidae were found in only 2 stomachs of this group and in none of the larger groups of cod examined. Caprellids occurred in only one stomach. The importance of caprellids and cumaceans as a food for small

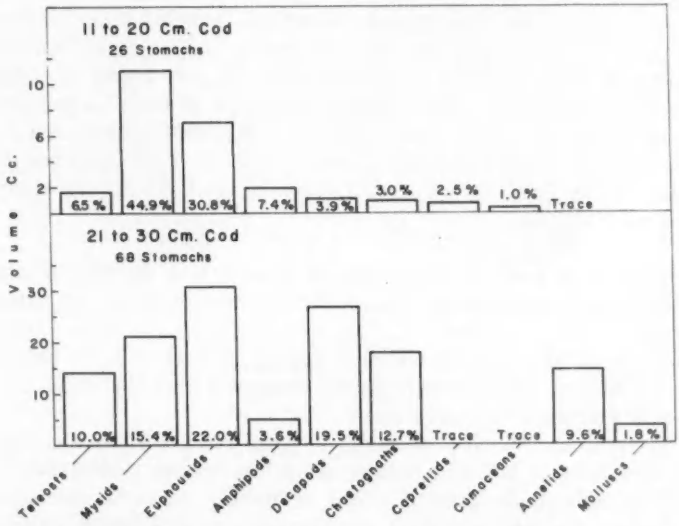

FIG. 8. Total percentages and volumes of food types found as stomach contents in 2 groups of small cod, 1956.

cod appears to be negligible. No molluscs or echinoderms were present in stomachs of this length group. Annelid remains, mostly setae and chitinous jaws, were found in only 2 stomachs from cod 19 and 20 cm. in length.

The quantity of fish taken in the diet increased in the 21–30 cm. size group. Young capelin (*Mallotus villosus*) and sand launce (*Ammodytes americanus*) were the most common fish ingested at this stage.

Accompanying the increase in volume of fish taken, there was a noticeable change in the types and volume of crustaceans eaten by cod. The total volume of crustaceans dropped from 90% in cod 11 to 20 cm. long to 60% in cod 21 to 30 cm. Mysids still appeared to be a very important part of the diet, but this prominent food item was superseded by slightly larger euphausids and decapods. *Meganyctiphanes norvegica*, absent from the stomachs of those fish 11 to 20 cm. in length, were first found, sometimes in considerable numbers, in cod 21 to 30 cm. long. *Thysanoessa raschii*, however, was the commonest euphausid found in these stomachs.

Decapods appeared to increase in this group of cod and a greater occurrence of larger species was apparent. Great numbers of *Pandalus montagui*, *Spirontocaris fabricii*, *Argis dentata*, and *Crago* sp. were found. Small hermit crabs

(*Pagurus acadianus*) began to make up an important part of the diet, but no true crabs were present.

It is noticeable that amphipods dropped in importance to about one half the value of that for the smaller size group of cod. There was a general increase in the number of amphipod species of larger size, although many of the smaller forms, such as *Melita* and *Hyperia*, were still plentiful. The largest types of amphipods found in the stomachs were *Anonyx nugax* and *Ceradocus torreli*. No copepods were found in these stomachs, and only traces of caprellids and cumaceans were present. Chaetognaths appeared in fairly large numbers, but were only found in a very small fraction of the total stomachs examined.

Annelids in the form of nereid worms and small sea mice began to occur regularly in the 21 to 30 cm. cod. Occasional molluscs appeared for the first time in cod of this size.

SELECTION OF FOOD BY SMALL COD. It appears that the diet of small cod is restricted to a limited number of food forms, in contrast to the varied diet of larger cod.

Corbeil (1954a) carried out an inventory of bottom fauna inhabiting the waters off Miscou Island, which can be compared with the small cod stomach analyses of the present investigation.

The single species most abundant in small cod stomachs was *Mysis mixta*, while from samples taken in bottom drags this species ranked third in actual number of individuals. Ranked ahead of mysids were the decapod shrimps *Argis dentata*, *Pandalus montagui*, and *Spirontocaris* spp. which, although found in considerable numbers in the cod stomachs, were not taken by the cod as often as their occurrence would lead one to expect if small cod restricted their feeding to the bottom. It is strongly suspected that this is not always the case.

The next most abundant dietary forms were euphausids and amphipods, while the bottom surveys show practically no euphausids and only low numbers of amphipods. Almost half of the amphipods found in the stomachs were pelagic like *Hyperia* and *Themisto* spp., which are not recorded for the bottom tows. This shows that these small fish feed pelagically to a great extent. Further comparisons show that certain benthic organisms which are found commonly in the stomachs of small cod are not listed for the bottom tows in this area. This appears to be the case with annelid worms and sea mice. It would appear that there is a greater selection of these two forms than their relative abundance in bottom drags would indicate. Echinoderms, on the other hand, appear to be taken less readily than their natural occurrence might warrant. Size may influence this selection to a certain extent, but bottom drags indicate that even small forms, such as *Ophiura sarsi*, are relatively abundant, and yet are found only rarely in stomachs.

When the sexes were analysed separately with regard to feeding habits, it was found that there was no appreciable difference between the diets of small male and female cod.

COD OVER 30 CM. IN LENGTH. Fig. 9 shows the results of volumetric analyses of the types of food found in 4 cod length groups. Discussion will be limited to a description of major changes in the varied diet of larger cod.

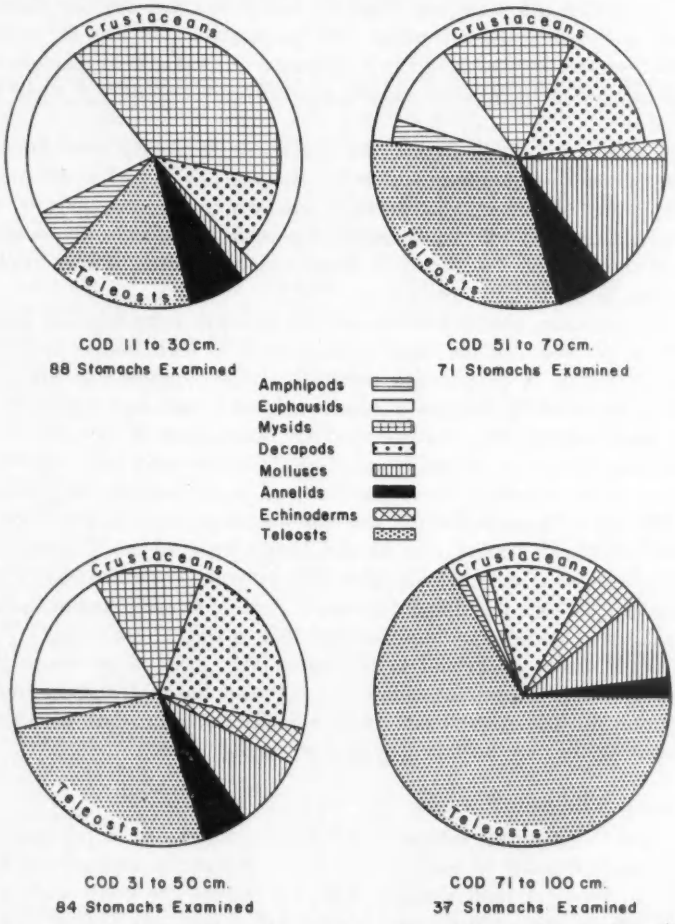

FIG. 9. Percentage volume of main food types in the stomachs of 4 length groups of cod, 1956.

The crustacean diet gradually decreased and decapods occurred as the most prominent crustacean, especially hermit crabs (*Pagurus acadianus*). Euphausids and mysids continued to be important groups until a length of 71 cm. was attained. In cod over 71 cm. many euphausids and mysids were found in stomachs along with such fish as herring, but their volume was relatively unimportant.

Molluscs contributed a great deal to the diet of large cod, and they reached their peak importance in fish 51 to 70 cm. long. The most common forms were the whelk, *Buccinum undatum*, and a pelecypod, *Yoldia* sp., but large numbers of bank clam, *Cytodaria siliqua*, were also found. Another mollusc should be mentioned, although it did not occur very frequently. This was the squid, *Ommastrephes* sp., which was found in 4 stomachs in 1955 and in 3 stomachs in 1956. It contributed a large share of the total volume, but only a small number of individuals.

Annelids and echinoderms, the next most important food items, occurred in approximately equal numbers in the stomachs of cod 31 to 50 cm. in length. Echinoderms were found in greatest numbers in the stomachs of the largest group of cod, 71 to 100 cm. in length. *Ophiopholis aculeata*, the common brittle star of the region, was found in large numbers, often tightly packed in the stomachs of these large cod.

Coelenterates, chiefly jellyfish, and ctenophores were taken in large amounts by the larger cod, but the high liquid content of their bodies made volumetric analysis difficult. A conservative estimate of their importance would be in the neighbourhood of 5%, but this would be subject to seasonal variations.

Volumetrically, fish was the most important part of the diet of large cod. In cod 31 to 50 cm. in length, it made up 25% of the total food ingested; in those of 51 to 70 cm. it formed 32% of the diet; and in the largest group, 71 to 100 cm., 69%. Herring (*Clupea harengus*) was the most important fish food. No cod below 40 cm. contained herring, but in cod larger than 40 cm. herring became increasingly more numerous. Blennies (*Pholis gunnellus*), shannies (*Leptoclinus maculatus*), included in Bleniidae, small plaice (*Hippoglossoides platessoides*), and sculpins (Cottidae) were observed first in cod 32 cm. long. It has already been noted that capelin and launce were taken by cod of the smaller length group. Mackerel (*Scomber scombrus*), cod and hake (*Urophycis tenuis*) were found only in fish over 60 cm. It is possible, however, that young individuals of these species may be taken by cod of smaller sizes.

Pelagic and Benthic Feeding

Table IV shows the estimated volumetric importance of pelagic and benthic organisms in the diet of cod of various size groups. It appears that the ratio of these two types of food changes with the size of the cod, small cod feeding mainly on pelagic animals and larger cod mainly on bottom animals. The actual rooting up of bottom fauna commences at lengths of 31–50 cm., at which length cod seem to take significant numbers of molluscs.

The tendencies towards pelagic feeding in small cod serve to explain their distribution within the area to a great extent. Small cod, 11 to 30 cm. in length, are seldom taken at depths over 30 fathoms, and then only in small numbers. They tend more towards inshore waters of 0–20 fathoms, where few commercial boats fish. In some areas (Thompson, 1954) even the large cod exhibit pelagic feeding habits by chasing capelin at the very surface of the water. In the southwestern Gulf of St. Lawrence mass feeding of this type occurs

very rarely, although there is limited feeding upon herring and capelin. However, even among large cod the diet is pelagic to a great extent, and diurnal vertical movements of fish of all sizes probably result. On dull days and at night, euphausids and mysids are believed to rise off the bottom. There would

TABLE IV. The relative importance of pelagic and benthic food forms in the diet of cod of different length groups, 1956. (A): semi-pelagic; (B): benthic; (P): pelagic; (D.W.): deep water; (S): surface; (I.S.): inshore; (N.I.): not identified.

Stomachs examined	Cod length groups									
	11–20 *cm.* 26		21–30 *cm.* 68		31–50 *cm.* 91		51–70 *cm.* 80		71–100 *cm.* 59	
	P	B	P	B	P	B	P	B	P	B
Mysidacea (A)	14	...	40	...	30	...	23	...	12	...
Mysis mixta (A)	(13)	...	(24)	...	(12)	...	(12)	...	(6)	...
Mysis stenolepis (I.S.)	(1)	...	...	...	(1)	...	...	...	...	...
Erythrops erythrophthalma (D.W.)	...	...	...	...	(1)	...	(3)	...	...	...
Euphausiacea (P)	12	...	38	...	48	...	29	...	20	...
Decapoda: Natantia (P)	2	...	22	...	35	...	29	...	19	...
Pandalidae	...	...	(10)	...	(8)	...	(9)	...	(11)	...
Hippolytidae (I.S.)	...	...	(4)	...	(5)	...	(7)	...	(1)	...
Cragonidae	(1)	...	(1)	...	(11)	...	(8)	...	(6)	...
Paguridae (B)	...	1	...	4	...	13	...	11	...	10
Cancridae (B)	...	...	...	...	...	...	...	3	...	3
Amphipoda (P)	10	...	24	...	38	...	37	...	16	...
Caprellidea (B)	...	2	...	3	...	4	...	...	...	...
Copepoda (P)	2	...	...	...	...	...	...	...	...	...
Cumacea (B)	...	...	...	2	...	...	...	...	...	...
Isopoda (B)	...	...	...	...	...	1	...	...	...	...
Insecta (S)	1	...	...	...	...	...	...	...	...	...
Coelenterata (P)	...	...	...	...	...	...	4	...	2	...
Ctenophora (P)	...	...	...	...	1	...	1	...	1	...
Annelida (B)	...	...	...	...	...	10	...	3	...	...
Polychaeta (B)	...	2	...	9	...	12	...	21	...	19
Sipunculida (B)	...	...	...	...	...	1	...	2	...	...
Echiurida (B)	...	...	...	...	...	...	...	2	...	...
Mollusca (N.I.)	...	...	...	...	...	6	...	6	...	3
Gastropoda (B)	...	...	...	2	...	9	...	18	...	14
Pelecypoda (B)	...	...	...	...	...	...	...	10	...	8
Cephalopoda (P)	...	...	...	...	...	...	1	...	2	...
Echinodermata (B)	...	...	...	2	...	10	...	7	...	5
Chaetognatha (P)	1	...	3	...	1	...	1	...	1	...
Ascidia (B)	...	...	...	...	...	1	...	4	...	1
Teleostei (N.I.)	2	...	6	...	7	...	9	...	7	...
Clupea harengus (P) (herring)	...	...	...	...	2	...	8	...	18	...
Pleuronectidae (B) (flounders)	...	...	...	...	...	4	...	9	...	9
Mallotus villosus (P) (capelin)	...	...	1	...	5	...	9	...	2	...
Osmerus mordax (P) (smelt)	...	...	...	...	2	...	2	...	1	...
Blenniidae (A) (blennies)	...	...	2	...	9	...	3	...	2	...
Cottidae (B) (sculpins)	...	...	...	...	...	2	...	2	...	1
Gadidae (A) (cod, hake)	...	...	...	...	...	...	2	...	3	...
Scomber scombrus (P) (mackerel)	...	...	...	...	1	...	1	...	1	...
Ammodytidae (B) (launce)	...	...	...	2	...	1	...	2	...	2
Hemitripteridae (A) (sea ravens)	...	...	...	...	...	...	1	...	...	...
Zoarcidae (B) (eelpouts)	...	...	...	...	...	...	...	1	...	...
Frequency of occurrence	44	5	136	24	179	74	160	101	107	75
P/B ratio	8.8	1	6.1	1	2.4	1	1.6	1	1.4	1
Total volume, *cc.*	20.7	1.8	112.1	24.8	472.9	221.7	1299.3	773.9	1240.7	1260
% volume	92	8	81.8	18.2	68.1	31.9	62.6	37.4	49.6	50.4

also be an upward shift of cod at night, since they are feeding on these crustaceans to a great extent. The extent to which this occurs cannot be estimated, since no night tows or tows at different water levels were made during this study. From the degree of decomposition of food in the stomachs, it is known that the cod must feed at night, and that the food forms taken then are to a great extent pelagic.

Geographic and Seasonal Variations in Diet

The stomach contents of cod caught in 4 different areas, namely Shippegan Gully, Miscou Island, Chaleur Bay, and Bonaventure Island (Fig. 1), were analysed to determine whether there were any outstanding differences between cod diets in these areas.

Nearly all the groups of animals sampled showed similar abundance in the stomach contents of these groups of cod (Table V). However, certain differences could be observed within the fish diet. Herring was the most important fish in the cod diet of every area except Shippegan, where it was surpassed by the great numbers of flounders, mainly small plaice. Herring were found most abundantly as food in the Miscou Island and Bonaventure Island regions, where they comprised 75% of the fish diet. In the other localities, Chaleur Bay and Shippegan Gully, herring constituted only about 25% of the fish diet.

Monthly variations in diet were noted for the 3-month period, June, July and August (Table VI). Annelids and molluscs appeared to remain constant during the summer months. The annelids showed no change throughout the summer, being present in about 20% of the stomachs. Molluscs remained at a uniform level, but were higher than annelids.

Table V. Local variations in diet between 4 areas in the southwestern Gulf of St. Lawrence, for cod over 30 cm. in length, 1956.

	Shippegan Gully 62 stomachs volume	Miscou Island 73 stomachs volume	Chaleur Bay 27 stomachs volume	Bonaventure Island 50 stomachs volume
	%	%	%	%
Annelida	5.3	1.9	2.3	3.2
Ascidia	2.1	0.6	11.9	...
Chaetognatha	...	trace	...	...
Coelenterata	1.0	13.8	...	13.0
Crustacea	33.0	29.4	32.4	34.4
Echinodermata	5.0	2.5	5.3	...
Mollusca	11.3	6.9	10.6	14.7
Teleostei: Total	42.3	44.9	37.5	34.7
Herring—*Clupea harengus*	25.9	72.7	26.4	78.2
Launce—Ammodytidae	0.4	0.6	...	...
Smelt—Osmeridae	6.1	3.0	14.0	15.1
Blennies and shannies—Blenniidae	4.3	2.0	16.5	4.7
Sculpins—Cottidae	0.8	0.5	11.7	...
Cod, hake—Gadidae	19.2	0.7	17.8	...
Flatfishes—Pleuronectidae	32.0	14.6	6.2	...
Mackerel—Scombridae	10.9	1.0	2.3	...
Eelpout—Zoarcidae	0.2	2.3	...	...
Not identified	...	2.1	4.8	2.1

TABLE VI. Monthly variation in the diet of cod, as measured by frequency of occurrence of organisms in the stomachs throughout a 3-month period.

	June			July			August		
	No. of individuals	No. of stomachs	%	No. of individuals	No. of stomachs	%	No. of individuals	No. of stomachs	%
Annelida	33	23	22.3	55	33	22.7	38	34	20.7
Ascidia	0	0	0	7	3	2.0	3	3	1.8
Chaetognatha	0	0	0	3	2	1.3	140	4	2.4
Coelenterata	2	1	trace	4	3	2.0	18	6	3.6
Crustacea									
Amphipoda	232	42	40.7	175	49	33.8	93	39	23.7
Decapoda: Reptantia	31	21	20.4	30	27	18.6	42	33	20.1
Decapoda: Natantia	59	27	26.2	108	40	27.5	94	60	36.3
Cragonidae	12	5	4.8	56	12	8.3	43	21	12.8
Hippolytidae	28	10	9.7	32	14	9.6	22	16	9.7
Pandalidae	10	8	7.8	14	10	6.8	19	14	8.5
Not identified	9	4	3.8	6	4	2.7	10	9	5.5
Euphausiacea: Total	...	...	41.7	...	...	35.1	...	...	36.5
Thysanoessa inermis	319	3	2.9	31	6	4.1	4	2	1.2
Thysanoessa raschii	667	10	9.7	80	18	12.4	167	13	7.9
Meganyctiphanes norvegica	145	7	6.8	51	9	6.2	375	30	18.2
Mysidacea	5,586	43	41.7	483	33	22.7	116	28	17.0
Echinodermata	52	14	13.5	199	20	13.7	82	16	9.7
Mollusca									
Cephalopoda	0	0	0	4	3	...	1	1	...
Gastropoda	34	21	20.3	53	26	17.9	34	27	16.4
Pelecypoda	6	4	3.8	12	9	6.2	7	6	3.6
Teleostei: Total	...	15	14.5	...	52	35.8	...	74	45.1
Clupea harengus	12	7	6.8	17	12	8.3	35	30	18.2
Total stomachs examined		103			145			164	

The percentage of crustaceans was practically constant throughout the summer, with, however, a slight decrease for the months of July and August. Amphipods, especially *Anonyx nugax*, were very numerous through June until the middle of July, but seemed to decrease during August. Of the euphausids, *Thysanoessa inermis* was most abundant in June, and *Meganyctiphanes norvegica* in August and September; *Thysanoessa raschii* decreased in August. Mysids occurred in the stomachs chiefly during the early part of the summer, after which their numbers declined.

There was an increase in the number of herring as the season progressed, but the percentages were not radically different. However, the increase in the total of fish as the summer advanced may be significant since the differences were great. In June the percentage of stomachs containing fish was 14, in July—35 and in August—45.

The fish diet of cod included the species shown in Fig. 10. Jean (1954b) investigated the relative abundance of various species of fish in the same area, using an otter trawl with 3-inch mesh. Although the smallest sizes of fish would not be retained, it does give a good indication of the relative numbers of the intermediate-sized fish in the area.

When compared with the frequency of fish types found in cod stomachs, it appears that herring, which ranked third in importance of natural abundance

on the bottom, appear at the head of the list of food fishes. Plaice occurs as the third most numerous fish in abundance and as food of cod.

Capelin was the second most frequent food fish in the diet, but no comparison was available to determine their relative abundance, since due to their small size they would easily slip through the mesh used by Jean (1954b). Capelin

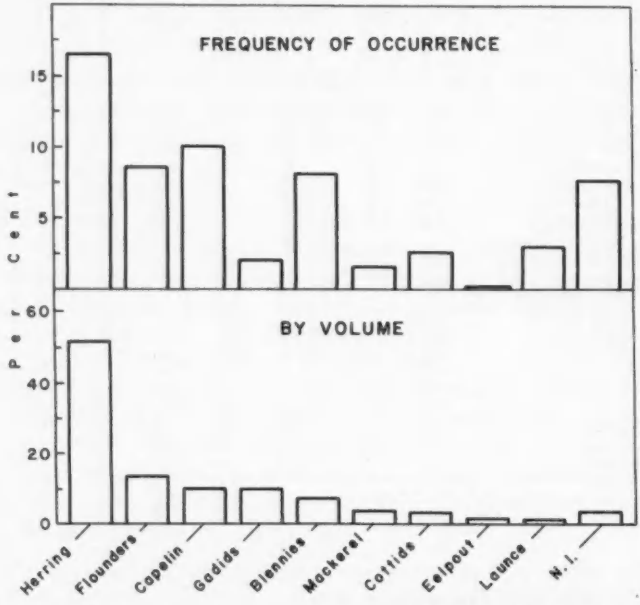

FIG. 10. Percentage frequency and volume of fish types found in 331 cod stomachs, 1956. (N.I. = not identified; see Table IV for the scientific names of the groups indicated.)

were found in the stomachs of cod of nearly all lengths. It appears probable that cod tend to select herring and perhaps capelin over cod and plaice.

Blennies and shannies occur as the next most frequent food fish, which compares well with natural abundance as estimated by Jean. Witch (*Glyptocephalus cynoglossus* L.), rays (*Raja* sp.), and sculpins (Cottidae) are not fed upon to the same degree as blennies and shannies, although their frequency of occurrence is just as great.

While analysing the frequency of fish in the cod diet, it was found that during the summer of 1955 the proportion of stomachs containing herring was higher than in 1956. Herring appeared in the stomachs of smaller cod to a greater extent in 1955 as well. In 1954 herring in the Gulf of St. Lawrence became infected with the fungus disease *Ichthyosporidium hoferi* (Leim, 1955). In 1955 the outbreak was at its peak, leaving great numbers of herring dead and

in a weakened condition. It is probable that this disease made them more available for cod to feed upon.

Growth studies showed an increase in the rate of growth in 1955 (Scott and Martin, 1957). Size-at-maturity studies (Fig. 2) showed a larger size at maturity in 1955 than for 1956. This larger size at maturity may also be attributed to heavy feeding on herring in 1955 (Table VII).

TABLE VII. Frequency of herring in cod stomachs in the south-western Gulf of St. Lawrence during the summers of 1955 and 1956.

Year	No. of stomachs	No. of stomachs containing herring	No. of herring	No. of herring per stomach
1955	116	33	54	0.47
1956	136	26	33	0.24

SUMMARY AND CONCLUSIONS

A gross examination of 1,874 Atlantic cod gonads was made during the summers of 1955 and 1956 in the southwestern Gulf of St. Lawrence. Males matured at a smaller size than females. In 1955 and 1956, 50% of the males were mature at 54 and 50 cm., respectively, while 50% of the females were mature at 57 cm. and 52 cm. No mature cod younger than 4 years were found. The greater size at maturity in 1955 is attributed to more intensive feeding on herring, made more available to the cod because of the epidemic of *Ichthyosporidium hoferi*. Herring were taken by smaller cod in 1955 than in 1956.

The peak of spawning occurred toward the end of June in both 1955 and 1956, but spawning fish were found from June to September. Fecundity studies made demonstrated that the number of eggs increased with increase in cod size, from 200 thousand in the case of a 51 cm. cod, to 12 million in a cod of 140 cm. in length. The faster-growing fish in an age group were more fecund than the slower-growing fish.

The stomach contents of 620 cod were analysed during the summers of 1955 and 1956. These cod ranged from 11 cm. to 140 cm. in length. Cod of 11 to 20 cm. fed primarily on mysids, euphausids and amphipods, apparently moving off bottom in pursuit of food organisms. Small cod did not begin to feed upon fish until they had reached a length of 20 cm., after which fish became noticeably more important in the diet.

The diet of small cod was restricted to a limited number of food forms, in contrast to a varied diet in large cod (over 30 cm.). Mysids (*Mysis mixta*), euphausids, and amphipods appear to be selected by small cod over other forms, such as decapod shrimps, when comparisons are made between stomach contents and bottom drags. Annelid worms and sea mice were apparently selected readily, whereas echinoderms were not selected by small fish.

Large cod (over 30 cm.) fed on fish, crustaceans, molluscs, annelids and echinoderms, with coelenterates and ascidians occurring to a lesser extent. Herring was the most important part of the fish diet, followed by capelin and plaice. Herring were plentiful in stomachs from Miscou and Bonaventure

Islands, whereas plaice were found in greater amounts near Shippegan Gully. There were no other significant geographic variations in diet.

Small cod, and to a lesser degree large cod, fed pelagically in the area studied. During daylight most of the feeding probably took place towards the bottom or on the bottom in the case of large cod. At night cod probably tend to rise upwards to feed on pelagic groups of crustaceans. Feeding habits appeared to be one factor determining pelagic and demersal distribution. Spawning behaviour may have been another factor responsible for movements, but no data were available for a study of this type.

Seasonal changes were not very obvious in the 3-month period, but the fish diet increased as the summer progressed, a factor possibly related to more concentrated feeding after the peak of spawning had passed.

ACKNOWLEDGMENTS

I wish to acknowledge with gratitude all those who have contributed their assistance to the present study. Special thanks should be accorded to Dr. W. R. Martin and Dr. F. D. McCracken, Fisheries Research Board of Canada, St. Andrews, N.B., for advice during the summer months; to Dr. D. M. Scott and members of the Zoology Department, University of Western Ontario, London, Ont., for guidance during the academic year; to Mr. Pierre Brunel, Station de Biologie Marine, Grande-Rivière, Qué., for identifying many of the amphipods; and to the captains and crew members of the *J. J. Cowie* and *Mallotus* for collection of data in the field.

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Movements of Brook Trout, *Salvelinus fontinalis* (Mitchill), Between and Within Fresh and Salt Water[1]

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ABSTRACT

Major movements of trout into Ellerslie Brook, Prince Edward Island, were in April, June–July, and November; and out in May and October to early January. Some movements were preponderantly in one direction; others involved trout making simultaneous movements up- and downstream. Mean length of trout in movements was 16.8 cm., predominantly age II. Trout were short-lived and few survived to make repeated movements. About 50% of trout making return movements did so within a month. Percentage of Ellerslie-reared trout which ran to salt water varied from 12 to 35 over a 6-year period. There was inconclusive evidence of a heritable propensity to sea-running. After descending into the estuary, few trout left for open coastal waters. Short-distance movements resulted in population shifts in the brook in summer which were not detected in traps at mouth of stream.

Movements of trout between fresh and salt water were very closely associated with rise and fall of the water level in the brook, but not with height of water. Movements in spring and early summer were into preferred temperature. Although marked changes in water level occurred, few trout moved in winter after becoming acclimated to a water temperature of 0°C. or in summer when brook was at temperature of final preferenda. Continuance of movement for some time after 0°C. was reached seemed related to slow rate of acclimation. Movements were both random and directed. For most movements trout appeared conditioned by temperature and stimulated by changing water levels. Trout moved largely at night. Other influencing factors were living space, maturation and spawning. Turbidity, salinity, tides, and handling were without apparent effects.

INTRODUCTION

The eastern brook trout moves into salt water from most coastal streams of eastern Canada. In the Maritime Provinces such movements occur in the Gulf of St. Lawrence area and along the eastern Atlantic seaboard of Nova Scotia, and

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to a less extent in the Bay of Fundy region. A knowledge of the movements of the brook trout between and within fresh and salt water is fundamental to the development of fish cultural practices for maintenance and improvement of the important sport fisheries for the species.

An investigation has been in progress at Ellerslie Brook, Prince Edward Island, since 1946 to assess the value of pond formation to improve angling on a stream from which trout run to salt water. Data have been obtained on the number, movements, and growth of the trout, and on their availability to anglers. This paper deals with the movements of trout during the 6-year period prior to pond formation in the summer of 1952. Some pertinent data obtained on later dates and at other places are also included. Movements of trout are described and discussed in relation to factors which may have had a determinative influence.

Preliminary notes on movements of brook trout between fresh and salt water at Ellerslie Brook have been previously published (Smith, 1948, 1951).

ELLERSLIE BROOK

Ellerslie Brook is a small spring-fed stream which is tributary to Malpeque Bay on the north shore of Prince Edward Island (Fig. 1, 2). The stream drains approximately 10 square miles (26 sq. km.) of woodlots and productive farm land. With tributaries it has a length in summer at low-water levels of about 6 miles (10 km.). At this season trout are found in 4½ to 5 miles (7 to 9 km.) of the total length.

The width of those parts of the stream inhabited by trout at low-water levels in summer varies from 2 feet (½ m.) near the headwaters to 5 to 10 feet (1½ to 3 m.) along the middle portions, and as much as 20 feet (6 m.) at some places on the lower sections. A few pools of about 3 feet (1 m.) in depth are encountered. However, the brook is shallow for the most part, with alternating riffles and pools.

Along much of the stream there is good cover for trout from overhanging alders, stumps and logs on the stream bed, and in undercuts along the bank (Fig. 2).

The underlying rock formation of the area is red sandstone with a carbonate matrix (Permo-Carboniferous). The stream bottom consists mainly of weathered sandstones in the form of sand, pebbles and small rocks over much of the length of the brook. Sandstones form the stream bed at a few points on the lower sections. Mud is common where flow is slow, particularly in the upper areas.

Flow, shade and the character of the bottom are not conducive to development of rooted aquatic vegetation and it is quite scarce. Aquatic mosses are encountered. Filamentous algae may become abundant in summer in localized open-water sections.

Mean annual precipitation in the region is about 40 inches (102 cm.). Ellerslie Brook is subject to sudden spates, but since the drainage basin is small, they are usually of short duration. Records obtained in 1953 and 1954 show the highest discharge as 345 cubic feet per second (Smith and Saunders, 1956). However, there were only 7 spates during these 2 years that exceeded 50 cubic feet

per second. Discharge may fall below 1 cubic foot per second in summer. Water levels were recorded daily to the nearest quarter of an inch after April 1947, except for certain winter periods. They are plotted in Figures 4, 5 and 6. Records were obtained from a gauge attached to a heavy metal stake driven into the bottom of a back-eddy just above the influence of tide.

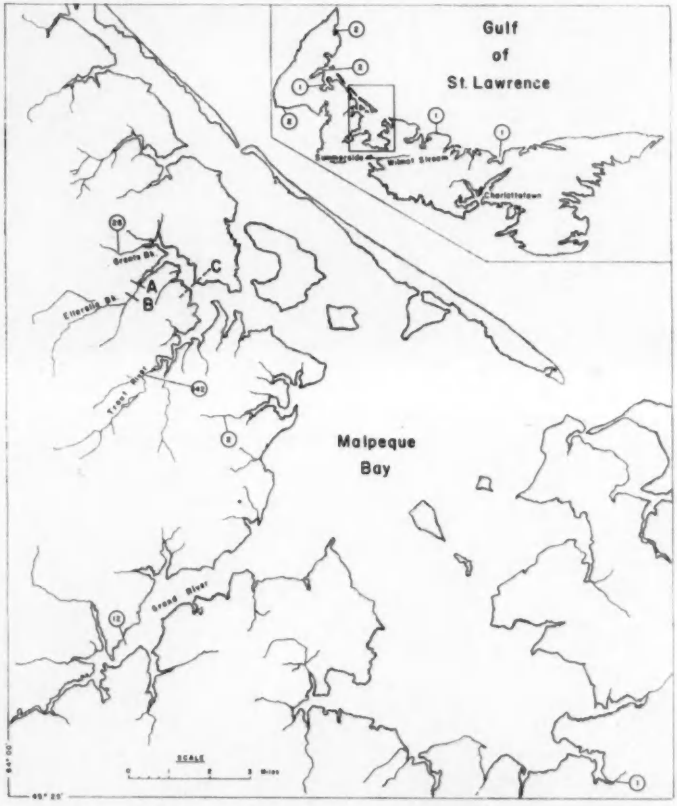


FIG. 1. Map of Malpeque Bay area, Prince Edward Island, with inset map of the province. Numbers of trout angled outside the Ellerslie System are given in circles. A and B indicate location of fences on Ellerslie Brook. C (broken line) indicates the arbitrary limit of the Ellerslie Estuary.

Prince Edward Island has a moderate climate. Mean annual air temperatures (at Charlottetown) of the region for the period 1910–1945 were: winter 20.1° Fahrenheit, spring 38.0°, summer 63.4°, autumn 47.4° (Whiteside, 1950).

Temperature of the water was recorded twice daily, about 9:00 a.m. and less regularly about 5:00 p.m. The recording station was located on the lower part

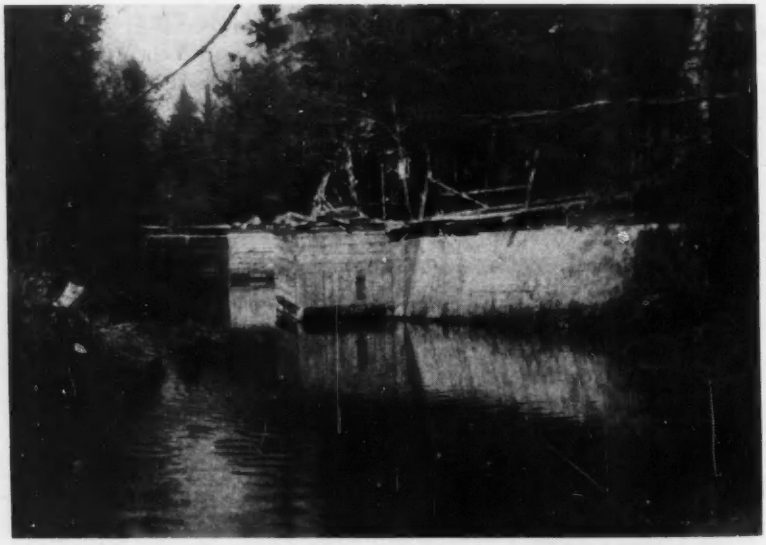


FIG. 2A (above). Stream fence, May 21, 1951.
FIG. 2B (below). Lower open part of brook, May 26, 1948.

FIG. 2C (above). An alder-bordered section of the brook, May 21, 1951.
FIG. 2D (below). Cover afforded by debris on middle section of the brook, May 21, 1951.

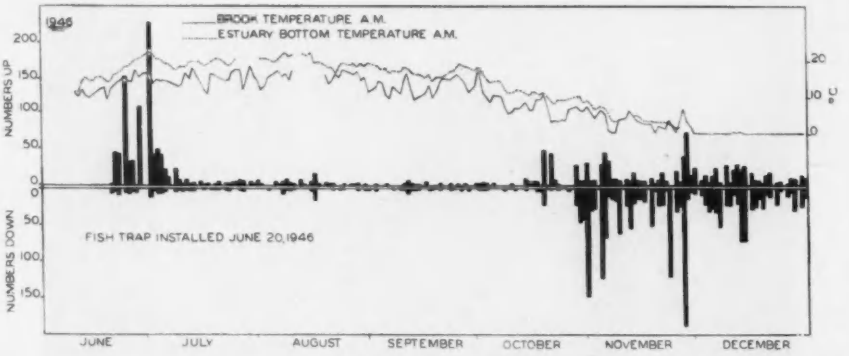


FIG. 3. Movements of trout through the estuarial traps on Ellerslie Brook, and morning temperature of water in brook and estuary, 1946.

of the brook immediately above the influence of tide. Morning water temperatures are plotted in Figures 3, 4, 5 and 6. Maximum water temperatures recorded in summer are presented in Table I. Water temperatures above 20°C. were encountered but such high levels were of very short duration. Night cooling was usually sufficient to lower the water temperature in summer to below 20°C. Mean morning water temperature in summer during the years 1947 to 1952 ranged from 11.6°C. in June to 18.4°C. in July (Table I).

TABLE I. Maximum recorded temperature, mean morning temperature and mean night cooling of Ellerslie Brook in summer.

	Maximum recorded			Mean morning			Mean night cooling		
	June	July	Aug.	June	July	Aug.	June	July	Aug.
	°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.
1947	20.0	24.8	25.0	11.6	18.4	15.9	3.2	3.8	3.1
1948	20.8	23.8	23.5	12.2	15.9	16.1	2.4	3.4	3.0
1949	22.0	25.0	21.8	13.8	16.3	15.3	3.5	4.6	3.6
1950	20.6	21.0	19.5	12.6	14.7	14.2	3.7	2.8	3.3
1951	18.8	20.6	19.2	11.6	15.2	15.4	3.0	2.7	2.0
1952	18.2	23.9	21.2	13.2	16.8	16.7	1.8	4.3	2.1

The stream is ice-covered for an average of 2 months during each winter.

The water is moderately hard. Conductivity of the water was 168 reciprocal megohms at 25°C. in July 1952. The determined pH range is 7.5 to 7.8 (Saunders and Smith, 1954). Leverin (1947) reports a chemical analysis of Ellerslie Brook water. He found the total hardness as $CaCO_3$ to be 93.9 ppm., and fixed CO_2 45.2 ppm., in samples collected on August 10, 1940. Calcium content was 33.8 ppm. Dissolved oxygen content was 9.4 ppm. (99% saturation) on the lower part of the brook on July 20, 1952. The brook receives considerable quantities of nutrient salts in the form of commercial fertilizers washed in from potato fields in the watershed.

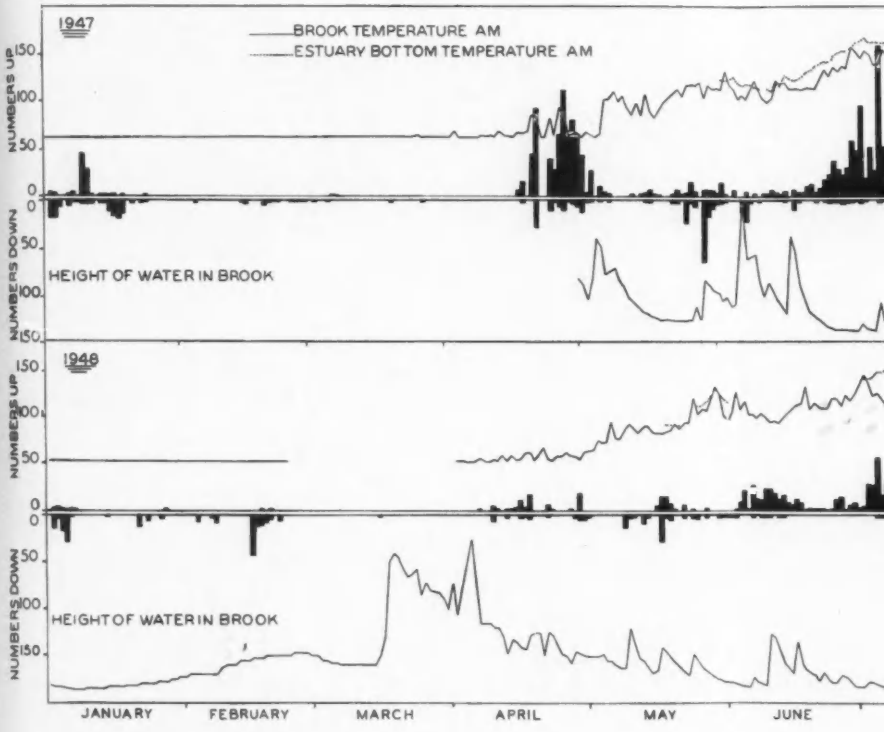
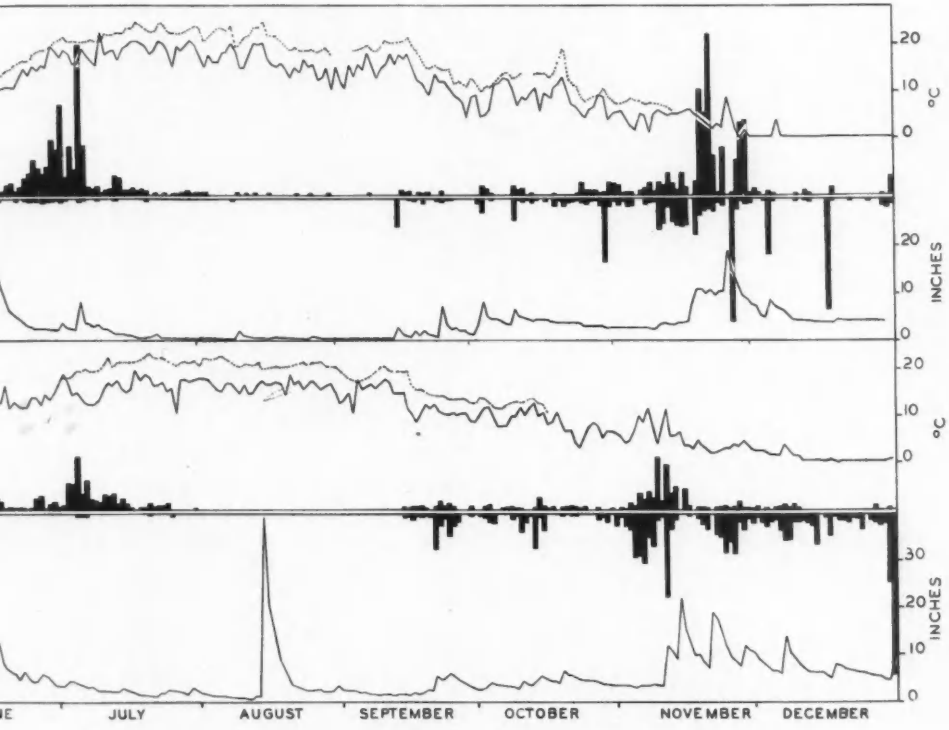


FIG. 4. Movements of trout through the estuarial traps on Ellerslie Brook, morning ten



orning temperature of water in brook and estuary, and water level in the brook. 1947 and 1948.

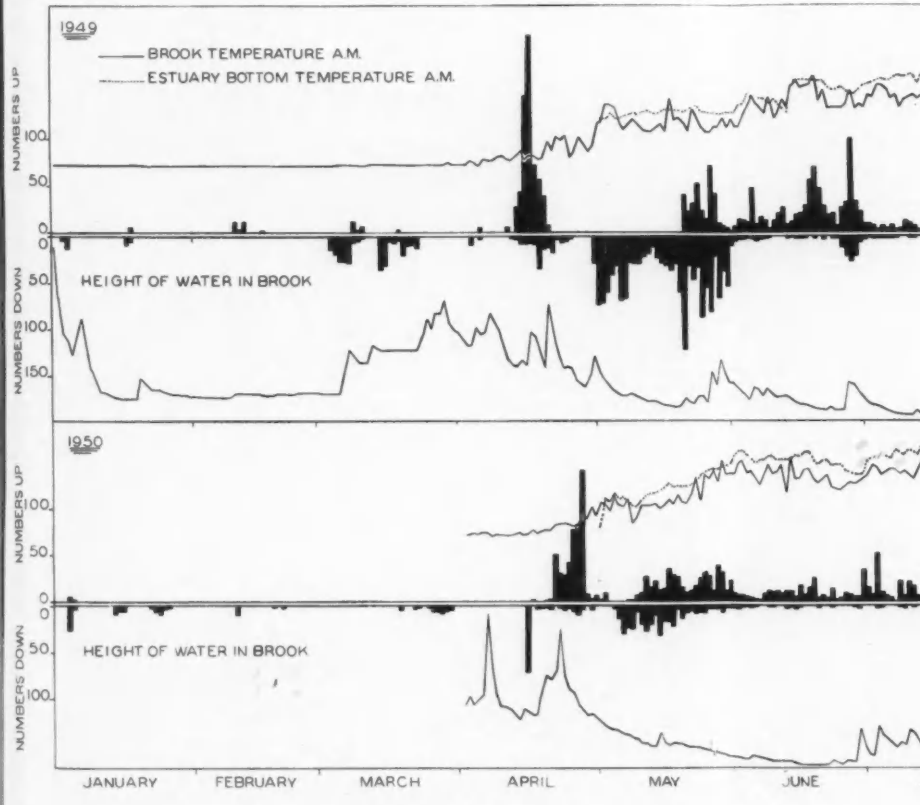
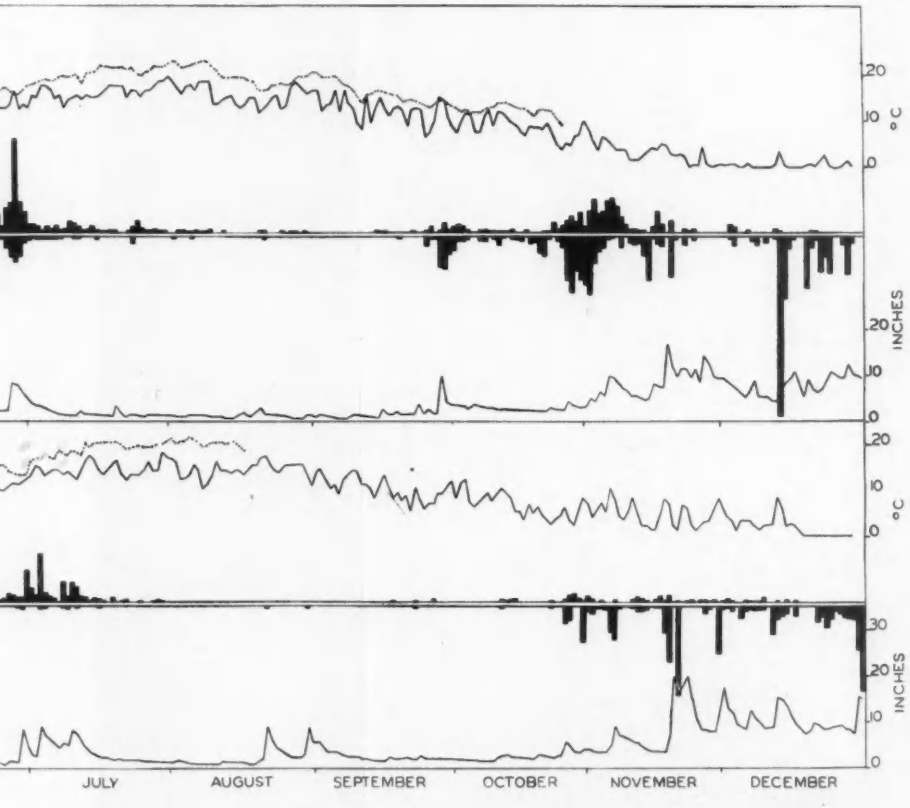


FIG. 5. Movements of trout through the estuarial traps on Ellerslie Brook, morning tempe



g temperature of water in brook and estuary, and water level in the brook. 1949 and 1950.

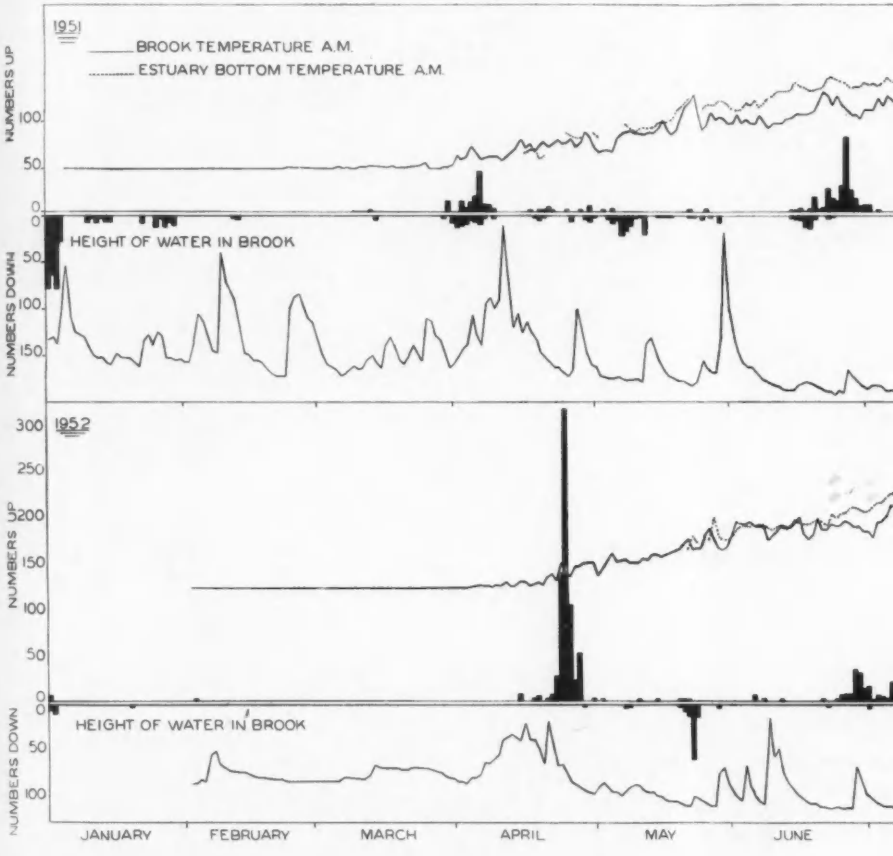
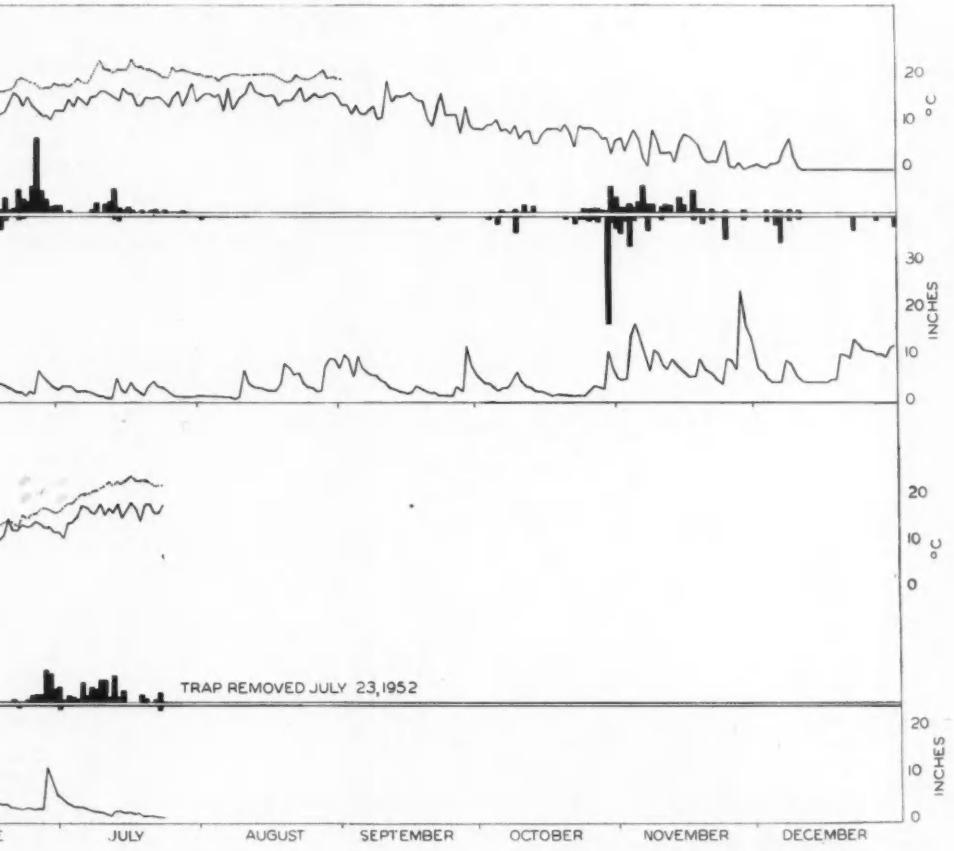


FIG. 6. Movements of trout through the estuarial traps on Ellerslie Brook, morning tem



rning temperature of water in brook and estuary, and water level in the brook, 1951 and 1952.

Aside from brook trout, the only other resident fish numerous in the stream before pond formation was young Atlantic salmon (*Salmo salar*). Salmon were distributed in the lower 3,000 yards (2,700 m.) of the brook. A few sticklebacks (*Gasterosteus aculeatus, Apeltes quadracus*) and small eels (*Anguilla rostrata*) also occurred. From the number of eels captured in sample sections of Ellerslie Brook by electrofishing in 1950 and 1951, the population for the entire stream was estimated at 200 and 60 respectively, for the 2 years (Smith and Saunders, 1955). Smelt (*Osmerus mordax*), tomcod (*Microgadus tomcod*) and occasionally a few gaspereaux (*Pomolobus pseudoharengus*) made spawning runs into the brook. Silverside (*Menidia notata*) and smooth flounder (*Liopsetta putnami*) were captured in the estuarial traps in early years of the investigation. White perch (*Morone americana*) were occasionally encountered at the brook mouth.

Trout predators frequenting the brook are kingfisher, great blue heron and mink. Of these, the mink is the most serious.

CONTIGUOUS SALT-WATER AREAS

The relation of Ellerslie Brook to the contiguous salt-water areas is shown in Fig. 1. The geography and hydrography of these areas have been discussed by Needler (1931, 1941). Discharge of fresh water into Ellerslie Estuary is not large except for an occasional heavy spate. Range in salinity in the estuary is about 23 to 29‰. Lower values are found only after heavy rains, and the usual range is 27 to 29‰. Needler (1931) writes: "Salinities of this sort are apparently the rule to within two or three hundred yards of the head of tide and the water may be over three-quarters at salt as that of the gulf outside even at the very heads of creeks which one can easily wade". The maximum surface water temperature in the estuary is about 25°C. Summer bottom temperatures taken at a depth of about 4 metres, approximately 1 mile (1.6 km.) from the head of the estuary are plotted in Figures 3, 4, 5 and 6. The estuary is ice-covered from 3½ to 6 months.

Malpeque Bay presents estuarial conditions and, hydrographically speaking, is the estuary of Ellerslie and other tributary streams. For this paper, however, the limits of Ellerslie Estuary have been arbitrarily set at about 2¼ miles (3.6 km.) from the head of tide (Fig. 1). Reference to Ellerslie System signifies brook and estuary to the above designated boundary.

Tides in Malpeque Bay have a small range of 2 to 3½ feet (0.6 to 1.1 m.). They are rather unusual in that when the moon is at its maximum declination north or south of the equator there is only one high and one low water in the day.

METHODS OF STUDYING TROUT

Capture

Trout were captured as they entered and left Ellerslie Brook at a counting fence (estuarial), situated about half-way between low and high tide levels (Fig. 1). This fence was put into operation on June 21, 1946. A second similar

fence (stream) was maintained after September 25, 1951, at a point on the brook 650 yards (594 m.) above the estuarial fence.

The fences consisted of a barrier and 2 traps, one to capture trout moving downstream, the other as they move upstream. The counting fences were not designed to capture trout fingerlings or the small yearlings. Trout to about 11 cm. (4 in.) fork length could pass through the spaces of ¾ inch between the rods and laths on the barriers and traps. However, most trout over 10 cm. in length would pass only with difficulty. The fences were operated throughout the year and tended daily. The efficiency of the year-round operation of the counting fences has been discussed by Smith and Saunders (1956).

Tagging

Trout captured at the fences were enumerated and fork length recorded. A serially-numbered monel metal strap tag was attached in circular form around the lower mandible of each fish (Smith, 1957). The adipose fin was also removed to aid in recognition of any recaptured trout that may have lost tags. Trout were first tagged at the estuarial fence on April 22, 1947, and at the stream fence on September 26, 1951.

Trout were also tagged when captured by seining and electrofishing during population studies in the stream during each summer since 1948. No fingerlings (age 0) were tagged, but adipose fins were removed.

Two sizes of tags (Salt Lake Stamp Company) were employed: 2×0.2 cm. and 3.5×0.3 cm. Average weight of the smaller tag was 0.08 gram, and that of the larger, 0.40 gram. The dividing point in length of trout in applying either small or large tag was approximately 14 cm. When a trout bearing a small tag was recaptured and had grown to exceed 14–15 cm. in length, the small tag was replaced by a large one.

From the time that tagging started in April 1947, through July 1952, 16,165 trout were tagged at the estuarial traps, at the stream traps, and during stream studies. Of these, 737 (4.5%) were recaptured after losing tags.

Recapture

Tagged trout were recovered at the two counting fences, by angling, during population studies in stream, in nets set in estuary and Malpeque Bay by commercial smelt fishermen, and by other means.

When tagged trout were recaptured at fences or during stream studies, tag numbers and lengths of fish were recorded before they were again liberated.

A creel census was maintained on Ellerslie Brook and its estuary during each angling season after 1946. A small reward was paid to anglers for tags, providing catches were submitted to creel-census taker for examination and measurement before tags were removed. Since area to be covered was small, these annual censuses were quite complete. The tagging program was publicized on Prince Edward Island by posters and newspaper notices. A notice of the program was printed for part of the investigational period on angling licenses issued by the Prince Edward Island Government. Further publicity was obtained at meetings

of branches of the Prince Edward Island Fish and Game Protective Association. These efforts resulted in records of tagged trout caught outside the Ellerslie System, and, as a result of the interest taken in the program by fishermen, were more complete than initially anticipated.

Trout were captured by smelt fishermen in gill- and box-nets set in estuary, ¾ to 1½ miles (1.2 to 2.5 km.) below the brook mouth. The smelt season was from October 1 to February 15. Record of the number of tagged trout captured in smelt nets was incomplete.

During the investigation 20 tagged trout were found dead along the brook. In addition 193 tagged trout were found dead in traps, killed by mink or by excessive water pressure. Seven small tags were found in a great blue heron killed at the stream fence on July 4, 1951. Tagging and recapture data revealed that five of the trout had been taken by the bird in the brook and two in the estuary. (Tags on trout fed to a captive juvenile heron were found in the bird when killed 23 days later.) However, there was no program of predator control and other records of this sort were not obtained.

Filing of Data

Field data for each tagged trout were transcribed to a punch card. The card is illustrated in Fig. 7. Sorting was done manually. Approximately 16,000 cards were involved in the investigation.

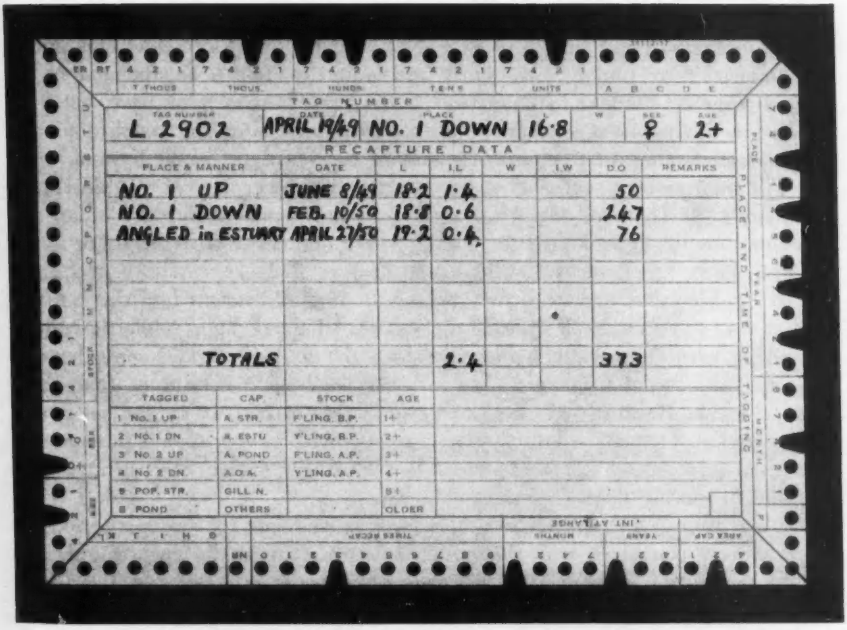


Fig. 7. Punch card employed in handling data on each tagged trout at Ellerslie Brook.

MOVEMENTS OF TROUT BETWEEN FRESH AND SALT WATER

We do not consider the movements of the brook trout in the Ellerslie System to be migrations. The following quotation from Allee *et al.* (1949), with reference to animals generally, express the situation pertinent to trout at Ellerslie Brook quite well: "Many seasonal movements, either between different strata of the same community or between communities of the same type, or between different types of communities, are difficult to classify as migratory in the strict sense of the word, or partially migratory, or not migratory". Thus, to avoid attempting to designate what movements of trout at Ellerslie Brook between and within fresh and salt water might possibly be called migrations, we will employ the word movements, implying thereby only what is explicit in the word when defined "as going from one place to another".

Number of Trout

Number of trout caught for the first time as they moved to sea through the estuarial trap during the period from June 21, 1946, to July 22, 1952, was 7,608; that for trout entering the brook for the first time was 5,992. Numbers by month and year are given in Table II in the B columns.

Number of Movements by Trout

Number of recorded movements by both tagged and untagged trout out of Ellerslie Brook during the investigation period was 10,883, and into the stream 11,556 (Table II). It has been shown by recapture of tagged trout that 21% of tagged individuals moving out of, and 23% of those moving into the brook got by the estuarial traps undetected (Smith and Saunders, 1956). Escapement of untagged trout is assumed to have been comparable. Corrections have not been applied in this paper since they would not materially alter any conclusions that will be forthcoming relative to movements of trout in the Ellerslie System.

The number of movements of trout varied from year to year (Table II). In the years 1948–51, there was good agreement between the numbers of up and down movements in each year ($r = 0.92$, with 2 degrees of freedom). For movements in both directions, the number was high in 1949, low in 1951, and intermediate in the other two years. Movements in 1947 did not fit into this pattern. In that year the number of upward movements was very high, while downward movements were comparatively low. Obviously the number of movements depends upon the number of trout available to move, and upon conditions that cause them to move. The summed effect of these factors in both fresh and salt water was to occasion similar trends in the years 1948–51 in the annual fluctuations. This occurred although different factors may have been determining, or may have operated in varying degree, in the two habitats.

When annual fluctuations in numbers of movements for various periods of the year were compared with those for the entire year, there was a highly significant correlation between the upstream movements in April and the yearly totals ($r = 0.95$, 4 degrees of freedom), as well as a significant correlation between those in June-July and the yearly totals ($r = 0.88$, 4 degrees of freedom).

TABLE II. Number of movements by brook trout through the estuarial traps, i.e., between fresh and salt water, at Ellerslie Brook. Column A—Movements by trout previously caught in estuarial traps, i.e., tagged or fin-clipped. Column B—Movements by trout not previously caught in estuarial traps.

	Jan.		Feb.		March		April		May		June		July		Aug.		Sept.		Oct.		Nov.		Dec.		Totals		Grand
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	totals
I. MOVING FROM FRESH TO SALT WATER																											
1946	...	...	...	...	...	...	...	...	...	...	18	39	25	35	20	21	21	8	44	261	258	727	211	381	597	1,472	2,069
1947	77	49	11	12	4	0	73	25	84	57	40	32	12	2	1	2	34	8	61	100	139	343	110	109	646	739	1,385
1948	40	52	49	56	1	0	18	16	30	44	8	13	6	1	0	0	31	85	36	114	130	474	173	377	522	1,232	1,754
1949	11	19	0	0	47	234	95	85	376	909	23	88	6	16	2	1	25	38	71	264	63	199	154	378	873	2,231	3,104
1950	21	52	5	10	13	32	31	92	111	235	10	19	5	5	1	0	2	0	55	25	117	231	58	303	429	1,004	1,433
1951	31	295	2	4	3	11	51	70	6	100	2	46	0	6	1	0	1	1	36	154	13	96	11	59	157	842	999
1952	2	22	0	0	0	0	0	2	45	61	3	2	1	1	...	...	...	...	...	...	...	...	...	...	51	88	139
Totals	182	489	67	82	68	277	268	290	652	1,406	104	239	55	66	25	24	114	140	303	918	720	2,070	717	1,607	3,275	7,608	10,883
II. MOVING FROM SALT TO FRESH WATER																											
1946	...	...	...	...	...	...	...	...	...	...	9	590	20	469	22	51	20	11	51	157	212	207	218	120	552	1,605	2,157
1947	49	55	0	0	0	3	381	253	83	52	139	211	228	306	5	9	16	5	50	50	298	512	22	12	1,271	1,468	2,739
1948	15	0	4	0	0	0	31	43	11	46	76	194	98	200	0	0	44	6	43	14	213	60	21	14	556	577	1,133
1949	4	2	14	13	22	1	406	212	292	32	621	149	84	46	15	6	17	7	95	42	110	127	12	10	1,692	647	2,339
1950	4	2	0	0	0	0	223	233	257	213	154	125	63	120	0	1	1	1	28	11	32	17	17	6	779	729	1,508
1951	0	0	0	0	7	5	52	29	6	1	115	118	31	53	0	0	0	0	71	6	63	130	5	5	350	347	697
1952	0	0	1	0	0	0	258	390	4	3	57	74	44	152	...	...	...	...	...	...	...	...	...	...	364	619	983
Totals	72	59	19	13	29	9	1,351	1,160	653	347	1,171	1,461	568	1,346	42	67	98	30	338	280	928	1,053	295	167	5,564	5,992	11,556

A greater or less number of movements in these periods presaged a similar fluctuation for the year. Such a degree of agreement was not found with respect to upstream movements at other periods of the year, nor with downstream movements at any period.

The maximum number of movements for any one year occurred in 1949 (Table II). In that year unusually large numbers of untagged trout, that is those moving for the first time, left the brook in March and May. There was also a comparatively large number of movements into the brook in April, May and June. These were preponderantly tagged individuals returning to the stream after only a short stay in salt water. However, the number of untagged trout—recruits from neighbouring streams and untagged escapees from Ellerslie Brook—that moved upstream during the year was in line with the numbers encountered in 1948 and 1950. In contrast to the situation in 1949, the number of movements in 1951 was the lowest recorded. Movements of trout, and fluctuations in their numbers, will be discussed later in relation to various factors.

Time of Year

Most trout moved between fresh and salt water during spring and early summer, and during fall and early winter (Table II, Fig. 3, 4, 5, 6). Although some trout were observed to move into and out of the stream in every month of the year, in general the numbers were small in midwinter and midsummer.

OUTWARD MOVEMENT. The most consistent outward movements to salt water were in fall and early winter—October, November and December. There was also a large movement out of the brook in the spring of 1949, notably during May. This movement was quite unique so far as numbers of trout were concerned. In May 1949, the number of movements by trout to salt water was 1,285, while the total number for this month during the 2 years previous and the 3 years after was only 773. Also aberrant from the general pattern were outward movements in February 1948, and March 1949.

INWARD MOVEMENTS. Most consistent and pronounced movements into Ellerslie Brook from salt water occurred in April, in June and early July, and in fall. Those in April, except in 1948 and 1951, involved several hundred trout each year. These movements were generally characterized by their short duration. Movements into the brook in the June-July period recurred annually, but with varying numbers of trout. Of all the movements, those in early summer are best known by fishermen, and are termed "strawberry runs". In May 1949 and 1950, larger numbers of trout entered the brook than usual, and the June-July movements were less clearly segregated. However, in these two years the April and May movements remained discrete as in other years. Inward fall movements were most prominent in November.

MOVEMENTS IN OTHER STREAMS. Two-way fish traps were maintained by us on Wilmot Stream, Prince Edward Island, from June 14, 1956 to January 4, 1957, and from April 17, 1957 to January 15, 1958 (Fig. 1). The situation is somewhat different from that at Ellerslie Brook. The fish traps were installed at the head of

the outlet stream from a pond. The outlet flows around one end of an embankment that holds the pond. Trout move freely up and down this outlet, which is short and enters the tidal estuary immediately below the embankment. The number of movements through the Wilmot traps is given in Table III.

TABLE III. Number of movements by trout through the Wilmot Stream traps.

	1956		1957	
	Up	Down	Up	Down
April	...	...	1	86
May	...	...	10	658
June	1,566	39	1,366	11
July	575	2	412	1
August	9	0	8	7
September	30	17	36	18
October	177	71	65	27
November	139	173	143	318
December	1	140	20	172

Common to both Wilmot and Ellerslie streams were the inward movements in June and early July, and in both directions during fall and early winter. In 1957, the one year in which observations were made in May, an outward movement occurred in that month. Early spring movements from salt to fresh water occurred at Ellerslie Brook during the latter half of April in most years, but was early in the month in 1951. With the Wilmot traps not in operation until April 17 in 1957, there remains the question whether an earlier spring inward movement occurred in that year. However, so far as comparable trapping permits comparison, we conclude that the pattern of movements in Ellerslie and Wilmot streams was quite similar.

White (1940, 1941) provides the most extensive data to be found in the literature on movements of brook trout between fresh and salt water. Two traps were maintained by him (primarily for salmon) during part of the open-water seasons in 1939 and 1940 on Moser River on the Atlantic coast of Nova Scotia. Both traps were situated about 1 mile (1.6 km.) above the estuary, one trap on the main river and a second on a tributary. In both years, movements of trout to salt water occurred in late April (minor) and in May, with return movements in July. In October 1939, White tagged adult trout moving downstream through the trap on the main river. Some were retaken shortly afterward moving upstream through the tributary trap. White (1940) seems to imply in his writing that the downstream fall movements were entirely within fresh water. Year-round trapping at head of tide on Moser River might have disclosed movements between fresh and salt water in early spring and during the fall months.

Huntsman (1938a) makes reference to the ascent of sea-run brook trout up Margaree River, Nova Scotia, during midsummer. Sea-run trout have been taken from this river by the junior author as early as May 24. Huntsman (1938a) also reports upstream movements of sea-run trout in June into Pomfret River, Nova Scotia. Salmon traps maintained about 7 miles (11 km.) above tidehead on

Northwest Miramichi River, New Brunswick, have captured good numbers of sea-run brook trout moving upstream in late May and during June (C. J. Kerswill, personal communication). An early summer upstream movement of brook trout into Maritime streams thus appears general wherever sea-running occurs. This movement is well known to fishermen, but there is less general knowledge of earlier or later movements. To illustrate, until year-round traps were maintained on Ellerslie Brook, the local public was unaware of upstream April movements.

In the more southern latitude of Cape Cod, Massachusetts, Bigelow and Schroeder (1953) report that brook trout ("salters") move from streams into salt water in November after spawning. They apparently remain in salt water for the winter, to return in April and early May.

Simultaneous Movements into and out of the Stream

On many of the days that trout moved by the estuarial fence they were taken in both the up- and the downstream traps (Fig. 3, 4, 5, 6). On some of these occasions movements were preponderantly in one direction. Examples are inward movements in April and in June–July. Recapture of tagged trout showed that the relatively minor number of outward movements at these times were, for the most part, by trout which had entered the stream only a day or so earlier. These trout apparently reversed the direction of their movement in the vicinity of the fence without going appreciable distances upstream. These short-distance movements in the fence area seemed to be quite random.

On other occasions, more equal and quite large numbers of trout were captured on the same day as they moved in opposite directions. Such instances occurred quite commonly during fall. An example is provided in Table IV where movements of trout captured at the estuarial fence on November 11, 1948 are analysed in light of subsequent recaptures. (Trout of same age and size were involved in both the up- and the downstream movements on this date.) As with inward movements in April and in June–July, some trout appeared to reverse the direction of their movement near the fence. On the other hand, the majority apparently proceeded well upstream or into the estuary, as was shown by the time lapses between captures and by places of recaptures. Whether the factors in the stream and estuary that caused the movements were the same or different,

Table IV. Movements of trout initially captured on November 11, 1948, at the estuarial fence.

	Moving up-stream	Moving down-stream
Number captured	47	89
Mean fork length (*cm.*)	16.7	17.1
Number not recaptured	12	23
Number recaptured	35	66
In estuarial traps within 3 days	1	13
" " " later in fall	22	11
" " " next year	7	32
Angled next year	5	4
Gill-netted later in fall	0	6

the effects of the initial stimuli were sufficiently strong to carry a good number of trout well past each other. This occurred although the trout were detained in the traps for periods up to 24 hours under comparable water conditions. However, the estuarial fence captured trout at only one point on the stream system. Accordingly, no data are available upon extent of reversal in direction of movement that may have occurred in stream or estuary before capture at the fence.

Size and Age of Trout

No detailed analysis of the growth of brook trout in the Ellerslie System will be presented. However, it is pertinent to this account to know sizes and ages in the population. Length frequencies among the trout that moved into and out of Ellerslie Brook during 4 seasonal periods—April, May, June–July, and fall through winter—are shown in Figures 8 and 9. Trout for all of the years 1946–1952 are lumped together.

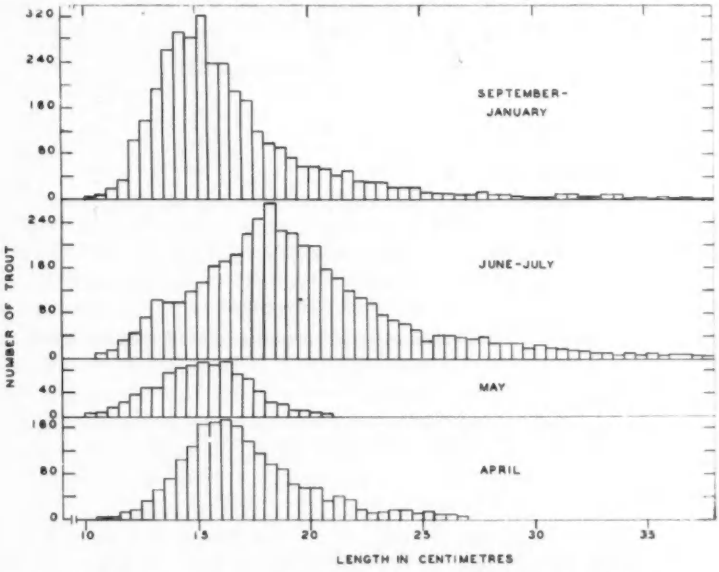


Fig. 8. Length frequencies of trout in the movements into Ellerslie Brook.

Average lengths at various ages are presented in Table V. Samples for age determinations consisted of trout angled in stream and estuary. In general, anglers retained the larger of the yearling (age I) trout. Thus, the average length for age I trout in Table V is probably high for the population of this year-class. However, the angled samples are considered representative for age II and older trout. No segregation is made in Table V between trout that had or had not been in salt water. It can be demonstrated that significantly faster growth was made by trout when in salt water.

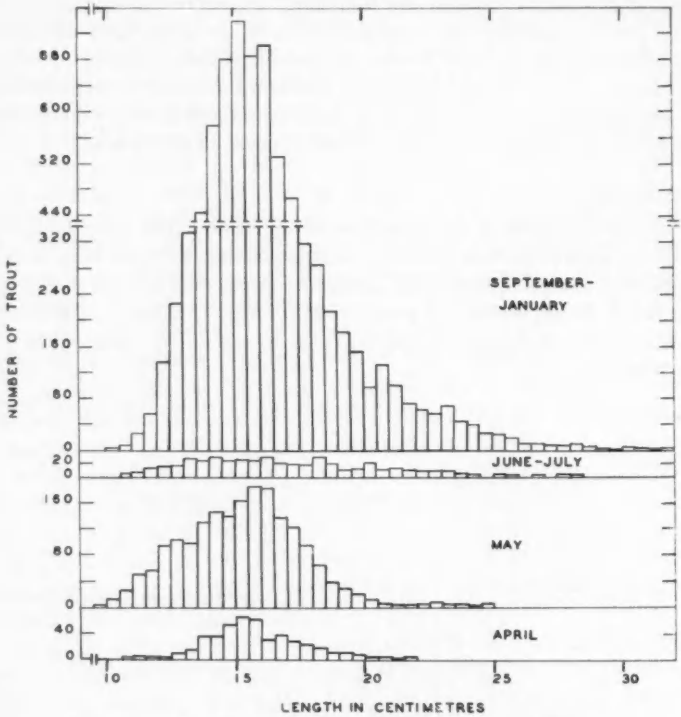


FIG. 9. Length frequencies of trout in the movements out of Ellerslie Brook.

TABLE V. Age and fork length in centimetres of angled trout at Ellerslie Brook. Numbers in samples given in brackets.

Year	Age I	II	III	IV
	cm. no.	*cm. no.*	*cm. no.*	*cm. no.*
1947	14.0 (19)	17.0 (515)	23.2 (94)	31.7 (1)
1948	14.9 (18)	16.6 (579)	21.6 (103)	27.2 (6)
1949	15.3 (38)	17.1 (938)	21.7 (90)	27.8 (2)
1950	14.6 (192)	16.7 (903)	22.1 (56)	24.5 (1)
1951	15.1 (35)	17.4 (809)	20.9 (156)	27.5 (2)
1952	14.0 (1)	18.0 (795)	21.2 (252)	26.3 (17)
1947–52	15.7 (303)	17.1 (4539)	21.6 (751)	26.7 (29)

The majority of trout that moved between fresh and salt water at Ellerslie Brook were small (Fig. 8, 9). Average fork length of trout that passed upstream and downstream through the estuarial traps was 16.8 cm. Average lengths of trout moving into and out of the brook were 17.6 and 16.0 cm. respectively. Average

length in the seaward movements was less since these movements consisted of a larger proportion of young trout going to salt water for the first time.

The largest trout were most consistently encountered in upstream movements in June–July and in fall (Fig. 8). They were more numerous in the former period. The mean length in the June–July movements was 19.4 cm. This mean fluctuated over the years (Table VI). (This situation obtained in varying degree with other seasonal movements.) It was high in the early years, fell to a minimum in 1949, and then rose again to the earlier level. The number of trout over 20 cm. in length in the June–July movements was highest in 1946 and 1947 (Table VI). In the

TABLE VI. Length of trout in the June–July upstream movements through the estuarial trap on Ellerslie Brook.

Year	Total number measured	Average length	Trout over 20 *cm.*		Trout over 25 *cm.*	
		cm.	*no.*	%	*no.*	%
1946	954	20.6	479	50	119	12
1947	953	20.7	367	39	200	22
1948	562	17.6	104	19	36	6
1949	901	16.8	156	17	35	4
1950	457	18.8	143	31	38	8
1951	309	21.3	190	61	42	14
1952	318	20.8	186	58	50	16

years after, the numbers of these larger trout fluctuated between 100 and 200. The annual variation in these numbers was not significantly correlated with variation in mean length of all trout in the movements. There was a significant correlation between the percentage of trout over 20 cm. in length in the June–July movements and mean length of all trout in the annual movements. Apparently the fluctuation over the years in mean length of the trout in the movements was relatively independent of the number of larger trout, but resulted largely from variation in numbers of young trout which were available to move, and did move.

Trout in the Ellerslie System were as a whole short-lived. Reference to Figures 8 and 9 and Table V shows that most trout moving between fresh and salt water were of ages I, II and III. Trout of age II were dominant. Individuals over 4 years of age were scarce.

For Moser River, Nova Scotia, White (1940) reports that 79.4% of the brook trout which ran to salt water in 1939 were age II, and the remainder were age III. Respective average lengths of these age-classes were 17.0 and 19.7 cm. White apparently found none moving to salt water at age I, such as were found at Ellerslie Brook.

As previously noted, trout shorter than about 11 cm. could pass through the spaces between laths and rods on the estuarial traps. From July 16 to October 28, 1947, these traps were lined with fine-mesh screening to ascertain if appreciable numbers of small trout were escaping. Of the 290 trout captured during this period only 2 individuals were less than 12.0 cm. We conclude that frequencies for the smaller trout in Figures 8 and 9 are quite representative.

Return Movements

NUMBER OF TROUT MAKING RETURN MOVEMENTS. Table VII shows the number of trout which were tagged in the estuarial traps as they moved out of or into Ellerslie Brook, as well as those which were tagged in the stream and were caught making their first movement to salt water. The number of these trout which made a return movement into and out of the brook is also given in Table VII. Fifty-seven per cent of the trout which went to salt water were recorded returning to the stream, while 27% of those running into Ellerslie Brook returned to salt water.

TABLE VII. Return movements through the Ellerslie estuarial traps by tagged trout after making their first movement either from fresh or salt water.

Number of trout making first movement	Number making one or more return movements	Percentage returning	Trout making the number of return movements indicated								
			1	2	3	4	5	6	7	8	9
	no.	%									
From fresh to salt water											
6,693	3,797	57	2,262	529	436	95	51	11	9	3	1
From salt to fresh water											
5,031	1,355	27	682	475	111	63	14	9	1	0	0

Failure by trout to make return movements can be ascribed in part to fishing mortalities. Creel censuses showed that 1,431 trout (28% of 5,031 which entered the stream) were captured by anglers in Ellerslie Brook, and 578 (9% of 6,693 which ran to salt water) in estuary and neighbouring streams without making a return movement. Capture in smelt nets set in Ellerslie Estuary accounted for an additional 331 (5% of 6,693) individuals, again without making a return movement. Records of fishing mortalities in smelt nets, and by angling in outside streams, are less complete than obtained by the creel censuses for Ellerslie Brook and Estuary. Trout were subjected to a much greater angling effort in the brook.

NUMBER OF RETURN MOVEMENTS MADE BY TROUT. The numbers of trout which made one, two or more return movements through the estuarial traps after having moved to salt water or into the brook for the first time are given in Table VII. The number which survived to make repeated movements between fresh and salt water was relatively small. The total number of trout counted on their first movements upstream or downstream was 11,724. Of this total, for instance, only 547 (5%) and 158 (1%) were subsequently retaken 3 and 4 times respectively in the estuarial traps. In extreme, 3 trout were recaptured 8 times, and one 9 times, in their movements between fresh and salt water.

TIME INTERVALS BETWEEN MOVEMENTS. Time intervals by monthly periods between ascent or descent and return of trout, as determined by recapture of tagged individuals, are given in Table VIII. A large proportion of return movements, whether from salt water or from the brook, was made within a short period of time. Thus, during the period that trout were tagged, April 1947 to July 1952,

TABLE VIII. Return movements of trout and intervals between movements through the estuarial traps at Ellerslie Brook.

Month	Movements Number[a]	Number of return movements at monthly intervals 0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12 and over
I. Trout which moved from fresh to salt water, April, 1947, to July, 1952														
January	545	17	1	25	45	14	18	5	...	...	2	...	...	2
February	126	4	1	9	5	9	2	...	...	1	...	...	...	2
March	341	39	51	24	15	...	...	...	1	...	...	...	...	1
April	558	73	58	35	1	...	...	2	1	1	...	...	...	...
May	2,058	582	321	24	3	1	3	2	...	...	1	...	5	11
June	286	160	7	3	...	4	1	...	...	...	...	1	1	...
July	61	32	...	...	1	...	...	...	...	1	...	...	...	...
August	8	3	1	...	...	...	...	...	...	...	...	...	...	...
September	225	91	10	3	...	...	...	7	1	2	5	...	...	...
October	916	365	22	3	...	...	27	23	16	17	2	...	...	1
November	1,805	491	4	3	3	64	88	34	50	6	...	1	2	1
December	1,732	44	3	1	138	162	81	69	6	...	...	...	2	3
II. Trout which moved from salt to fresh water, April, 1947, to July, 1952														
January	47	5	2	1	2	...	...	...	...	...	...	...	...	...
February	32	7	3	3	3	...	...	...	...	...	...	...	...	...
March	35	4	3	1	...	...	...	...	...	...	...	...	...	...
April	2,511	405	64	...	...	1	1	5	16	20	4	...	5	7
May	1,000	50	4	3	...	9	19	23	21	8	...	2	2	1
June	2,033	57	...	13	60	64	60	55	8	7	12	4	2	3
July	1,425	26	3	55	60	53	41	9	4	9	7	4	2	1
August	36	1	4	...	3	...	...	...	...	...	1	...	...	...
September	97	18	12	11	3	...	...	1	1	1	...	...	...	...
October	410	73	37	11	2	...	2	4	5	...	...	...	...	3
November	1,562	209	109	29	11	11	22	10	1	...	...	1	2	7
December	124	24	2	1	3	7	5	...	...	...	...	...	...	...

[a]Number of movements, including those of trout that moved through the traps more than once.

55% of return movements from salt water were made within a month, and 45% of those from the brook were within the same short period.

Trout that ran to salt water in spring and early summer, and returned to the brook, did so preponderantly within the same period (Table VIII). There were few return movements later in the year.

About half of the return movements made by trout which went out of the brook during fall and early winter also occurred within a month. Almost all of other return movements were made in spring and early summer after the trout had wintered in salt water. Short-term movements amounted to 40% of the total return movements made by the trout which left the brook in September and October, but only 3% by those which left in December and January. The closer the season of winter water temperatures, the greater was the tendency for outward-moving trout to remain in salt water. Trout which moved out in fall and early winter and did not return until next spring or early summer were, in largest numbers, those fish which made the longest continuous sojourn in salt water. These trout remained out of Ellerslie Brook from 5 to 7 months. Only relatively few trout stayed continuously for longer periods in salt water. Reference to Table VIII shows that there were only 71 movements by trout with an interval of 8 or more months between moving out and in.

Most return movements by trout which entered the brook in April were within 1 or 2 months (Table VIII). As the season progressed into May, June and July, an increasing proportion of the inward-moving trout stayed in the brook until fall before again running to salt water. Of the trout ascending the brook during fall, the majority that made return movements did so within the same period.

Statements in the preceding paragraphs imply that trout which left Ellerslie Brook, and returned, had spent the entire intervening time in salt water. This was not always the case as will be more fully discussed below under movements in salt water. It is suffice to note here that in two instances Ellerslie-tagged trout were taken in Trout River, released, and again recaptured at Ellerslie Brook (Fig. 1). Thus, unknown numbers of trout which left Ellerslie Brook, and returned, spent part of the intervening time in other fresh waters. On the other hand, trout apparently remained continuously in salt water over winter at least. Ellerslie-tagged trout were taken as late as February in smelt nets set in the estuary. Assuming that these trout behaved in relation to other streams in the area as they did to Ellerslie (i.e., little movement between fresh and salt water in winter), they remained in salt water until spring and early summer. We have noted from Fig. 8 that a major proportion of the largest trout which entered Ellerslie Brook came in during June and early July. Few trout of these larger sizes were found resident in Ellerslie Brook (Fig. 10). As previously indicated, trout grew significantly faster in salt than in fresh water. Trout, especially the larger, which entered the brook in June and July were those most heavily infested with parasitic copepods ("sea lice"). Thus, the evidence is that the larger trout at least had spent much of their time in salt water, and likely for continuous periods of several months.

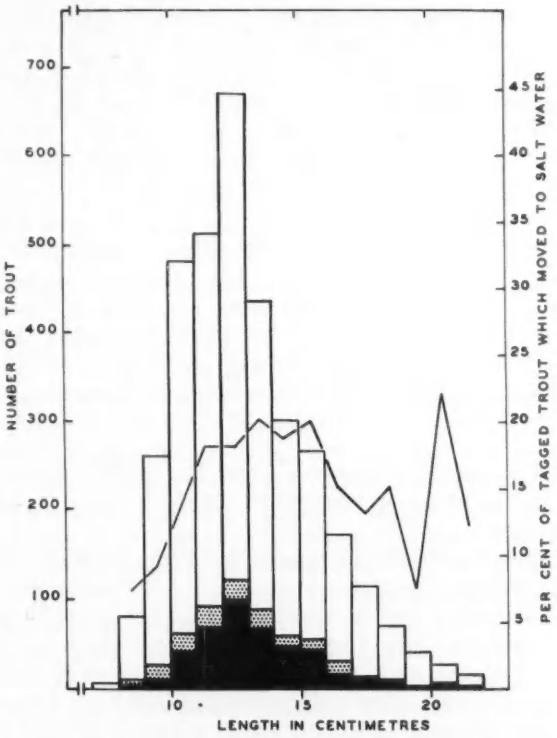


FIG. 10. Length frequencies of trout captured and tagged during summer in Ellerslie Brook. Solid black areas show number of trout which ran to salt water during fall of tagging; stippled areas, the number which ran during the following year. The percentage of tagged trout in each length frequency which ran to salt water is indicated by the line. 1948–51.

PROPORTION OF ELLERSLIE-REARED TROUT WHICH RAN TO SALT WATER

Assessments of trout populations in a number of 50-yard (46 m.) sections of Ellerslie Brook were made each summer, starting in 1948. The number of sections assessed from 1948 through 1951 were respectively 19, 23, 26 and 31. These embraced from 13% to 21% of that length of the brook and its tributaries which supported trout during the summer months. Pools and riffles, open and sheltered areas were represented. Assessments were made in July, through August, and into early September. Yearling and older trout captured during these studies were tagged.

From 1948 through 1951, 3,580 trout were tagged in Ellerslie Brook (Table IX). These had not previously been to salt water. Recapture of these tagged trout in the estuarial traps provided information on the proportion of trout reared in

the stream which moved to salt water. Of the 3,580 stream-tagged trout, 445 (12.4%) were taken in the estuarial traps during the fall of the year in which they were tagged. In addition, 150 (4.1%) individuals moved to salt water later, usually during the following spring. Reference to Table IX shows that in the years 1949, 1950 and 1951 roughly the same percentage went to salt water. However, the relatively high percentage in 1948 indicates that no constancy in this respect should be expected.

TABLE IX. Proportion of trout tagged in Ellerslie Brook during summer population studies which ran to salt water.

	1948	1949	1950	1951	Totals
Number tagged	570	985	708	1,317	3,580
Number running to salt water	199	148	82	166	595
Percentage running to salt water	34.9%	15.0%	11.6%	12.6%	16.6%

The combined data show that only a minority (16.6%) of the stream-tagged trout, which we consider representative of the trout reared in Ellerslie Brook, moved to salt water.

Length frequencies among the trout tagged in the stream, as well as number and percentage of trout in each size group which ran to salt water, are shown in Fig. 10. Fig. 9 illustrates that appreciable numbers of trout did not move into salt water until they were 12 to 13 cm. in length. Trout which were tagged in the brook and moved into salt water were no exception in this regard. However, trout of shorter length, to 12 cm., were well represented in the summer stream population when tagging was done (Fig. 10). Trout which were tagged in the summer and moved out of the brook in the fall of the same year increased on the average 2.0 cm. (0.0–5.1 cm.) in length during the intervening period. Accordingly, growth was sufficient by fall to bring a majority of the smaller trout (age I) encountered in the summer population to a size which ran to salt water. Only for the smallest yearlings would this not obtain, and when they did become large enough, say during the next spring, mortalities had materially reduced their numbers. Thus, we note in Fig. 10 that the proportion of trout 8 to 11 cm. in length in summer, and which ran later to salt water, was lower than for fish somewhat larger. The percentage of trout in length frequencies from 11 to 16 cm. (age I and II) which ran to salt water remained relatively constant at about 19%. However, the percentage of sea-running individuals among the larger fish (ages II and III, over 16 cm.) fell. Doubtless many, if not most of these larger trout would spawn in the fall of the year in which they were tagged. It is suggested that an increased mortality attendant upon spawning conditioned the lower percentage of these trout moving to salt water. Reference to Fig. 10 shows that all trout over 17 cm. which went to salt water did so in the fall of the year of tagging. Presumably most, if not all, of these older trout surviving at that time, and remaining in the brook, died during the following winter period.

SEA-RUN AND FRESH-WATER BROOK TROUT

Trout run into salt water from most coastal streams of eastern Canada. Sea-run individuals from a given stream when caught in salt water, or as they return to the stream, differ in appearance—form and coloration—from trout which have never, or have not recently, been in salt water. White (1940) and Wilder (1952) describe form and livery of sea-run trout. One characteristic most often noted is their silvery (guanin crystals) appearance in salt water. As pointed out by Wilder (1952), and observed by us at Ellerslie Brook, the silvery coating is reduced, if not lost, by sea trout after a few weeks in fresh water. Thus, sea-run trout captured in Ellerslie Brook during the summer population studies could not have been segregated except that they had been tagged.

Because some brook trout in our streams move to salt water, and there take on a more or less characteristic appearance, it is popularly held that there are two separable groups. It has been speculated by ichthyologists that sea-running may be based on genetic differences. This view would appear untenable on the *a priori* grounds that in a stream such as Ellerslie adequate isolation in spawning would not continue over a sufficiently long period to maintain the genetic integrity of different groups of brook trout. Where critical studies have been made, this appeared to be the situation. Wilder (1952), in his detailed study of sea-run and fresh-water populations of brook trout in Maritime waters, found no evidence "to indicate hereditary differences in migratory behaviour". He writes further: "Evidence available indicates that sea- and fresh-water trout of Moser River, Nova Scotia, constitute one taxonomic group".

Hubbs (1926) designated the sea-run brook trout of the Cascapedia River, Quebec, as a subspecies, *Salvelinus fontinalis hudsonicus* (Suckley). Later, Hubbs and Lagler (1949) only provisionally identified Cascapedia trout as a subspecies.

Sea-run brook trout have been prevented by dams from entering certain Prince Edward Island streams over extended periods. Streams above dams remain well populated with what might be called "freshwater" brook trout. None has been to salt water, nor have their progenitors, for a number of generations. In 1947, eggs were collected from and fertilized by parent "freshwater" trout from Eliot River, Prince Edward Island. A dam had existed continuously at the mouth of this stream for about 20 years. Also in 1947, eggs were collected from parent trout which had been to salt water at Ellerslie Brook. Both lots of eggs, kept separately, were incubated and the young reared under similar conditions at a hatchery. Approximately equal numbers of the progeny from both stocks were planted in Ellerslie Brook at age 0 and at age I. They were planted in early September along the middle section of the stream, after being differentially marked by fin-clipping (adipose and one of the paired fins).

Wilder (1952) studied the relative size of body parts of these two lots of trout when they were age 0. He found no differences in these respects that could be interpreted to be hereditary. He pointed out that the Ellerslie and Eliot trout "differed much less in body form than did two lots of trout of common parentage reared at different temperatures".

After planting them in Ellerslie Brook, the observation was made that trout from both the Ellerslie and Eliot stocks ran to salt water (Table X). However, the Ellerslie stock moved to salt water in larger numbers, and in greater proportion than the latter. Also the proportion of trout that returned to the stream was somewhat larger for the Ellerslie stock. All trout which ran to salt water from both stocks were over 14 cm. (Table X). This observation is in keeping with what was generally noted for trout which left Ellerslie Brook for the first time (Fig. 9). A small bias toward a faster growth rate on the part of the Ellerslie stock could have given rise to the observed results. However, the data in Table X do not support this view. The average length when running to salt water was not consistently greater for the Ellerslie stock. On the whole the data point to some hereditary influence on the sea-running of the trout, but the evidence is not conclusive.

TABLE X. Results of planting hatchery-reared progeny of Ellerslie and Eliot trout in Ellerslie Brook.

		Planted at age 0 1948		Planted at age 1 1949	
		Ellerslie	Eliot	Ellerslie	Eliot
Number planted		1,682	1,638	764	915
Number running to salt water	1949	13	3	88	56
	1950	46	13	79	21
	1951	7	4	6	2
Percentage running to salt water		3.9	1.2	22.6	8.6
Number returning to fresh water		41	11	123	49
Av. length[a] (*cm.*) when planted		5.2±0.66	5.6±0.61	12.5±2.09	12.5±2.02
Av. length[a] (*cm.*) when running to salt water	1949	14.6±1.43	15.5	15.2±1.56	14.5±1.69
	1950	15.9±1.73	14.4±1.42	14.9±1.73	15.4±2.62
	1951	17.4±1.46	17.0	15.9	20.7
Number captured in stream, not previously to salt water	1949	68	79	...	...
	1950	21	24	19	24
	1951	0	3	2	4
Av. length[a] (*cm.*) when captured in stream	1949	9.8±1.99	10.3±1.30	...	...
	1950	13.5±1.07	13.2±1.49	13.4±1.32	13.0±1.43

[a]With the standard error of the average.

Effects of pond formation at Ellerslie Brook upon movements of brook trout out of and into the stream is subject matter for another publication. However, some observations are pertinent to our present discussion. Thus, it was found that the pond held downward-moving trout to the extent that runs to salt water were markedly reduced, and in certain periods of the year were almost eliminated. During November and December, 1952, and January 1953, 1,160 trout moved down through the stream trap into the pond. During the same period only 10 individuals moved through the estuarial trap into salt water. An additional 79 individuals moved to salt water at later dates. These data are to be contrasted with those pictured in Figures 3, 4, 5 and 6 for the stream before pond formation.

Data obtained at Ellerslie Brook, as well as those reported by other investigators, notably Wilder (1952), argue in support of a contention that movements

of brook trout from fresh to salt water are basically no more than meeting the requirements of trout, with growth, for larger and more suitable living quarters. When a pond that presents a suitable environment is interposed, as was done at Ellerslie, between the stream and salt water, it assumes the function of the larger habitat formerly encountered only in the sea. There appears no need to postulate races of brook trout with heritable differences to explain their seaward movements and occurrence in salt water.

MOVEMENTS IN THE BROOK

In Relation to a Pool over a Short Summer Period

The population of trout in a pool was determined before and after approximately a month period in the midsummers of 1951 and 1952. The pool is about 90 feet long, 15 feet in maximum width, and 2 feet in maximum depth (1 ft = 0.305 m.). Much of the pool is open, but the upper end is well sheltered by overhanging alders. It is 2,700 feet upstream from the estuarial trap, and 750 feet above the stream trap.

Trout were captured by electrofishing. This method has proved to be highly effective in Ellerslie Brook (Saunders and Smith, 1954). Barrier nets were placed at head and foot of pool during fishing. All yearling (age I) and older trout which were captured in the initial assessments were tagged. No trout of the year (age 0) were found in the pool on those occasions. (There were 2 salmon parr and 2 eels in 1951 and 3 of each species in 1952.)

Data obtained from the population assessments are summarized in Table XI. Considerable movement of trout out of and into the pool obviously occurred. As a result of movements and mortalities, only a small percentage (14% in 1951 and 13% in 1952) of the trout originally in the pool were present at the end of the month period. Newcomers outnumbered originals approximately 2:1. It may be questioned whether electrofishing and tagging stimulated trout to move from the pool or caused mortalities. We have no evidence of this. In any event, trout which entered the pool were not similarly treated.

Table XI. Short-term changes in the population of yearling (age I) and older trout in a pool in Ellerslie Brook in mid-summer.

	1951		1952	
Number initially in population	July 9	183	July 15	151
Number recaptured:				
In pool at second assessment	Aug. 14	26	Aug. 13	19
By angling in pool	July 9–Aug. 14	11	July 15–Aug. 13	25
Running to salt water	July 9–Aug. 14	2	July 15–Aug. 13	0
Within stream	July 9–Aug. 14	2	July 15–Aug. 13	2
By angling in traps, and in stream (outside pool)	After Aug. 14	37	After Aug. 13	30
Number not recaptured		105		75
Number of new trout into pool	July 9–Aug. 14	48	July 15–Aug. 13	44
Number in population at second assessment	Aug. 14	74	Aug. 13	63
Net decrease in population	July 9–Aug. 14	109	July 15–Aug. 13	88

Population assessments in the pool were made in midsummer when few trout moved from the brook into salt water (Fig. 3, 4, 5 and 6). In 1951 and 1952 only 6 trout from the pool moved down during the month periods through the stream trap, and of these, 2 continued their movements to salt water. It is apparent that movements out through the estuarial trap in midsummer provided no index of the activity of trout at this season in the stream above. The results suggest that movements from the pool during the month periods were largely for short distances.

Movements between Estuarial and Stream Fences

The fences are 650 yards (594 m.) apart. The intervening stream area presented a favourable environment, particularly for yearling and older trout. This area provided the largest habitats, such as pools, in the freshwater part of the Ellerslie System.

Yearlings or older trout were not released from traps at either fence without being tagged. Both sets of traps were tended in morning except on a few occasions. Accordingly, the shortest period that could be recorded for movement of a trout up or down the stream area between traps was one day.

Daily movements of trout through stream and estuarial traps are compared in Fig. 11. Usually when either downstream or upstream movements were observed at one set of traps, contemporaneous movements in the same direction were also noted at the other. There were short-term periods, however, such as in early April and late May, 1951, when trout were found moving down through the stream traps but not the estuarial traps. Fig. 11 shows that most often the number moving down through the stream trap was larger for a given period than that which went to salt water in the same interval of time. Other periods can be selected when this situation was reversed. What occurred is more fully elucidated by tracing tagged trout in their movements in relation to the two fences.

Table XII. Movement of tagged trout into and out of stream area between the two counting fences (stream and estuarial) during specific periods.

I. Moving Downstream	Sept. 26, 1950 to Feb. 12, 1951	Oct. 8, 1951 to Jan. 2, 1952
Stream trap down	1,591	299
Stream trap up	107	18
Stream trap down, then through estuarial trap down into salt water	759	61
Stream trap down, but not to salt water	725	220
Total estuarial trap down	1,117	395
Estuarial trap down, but recruited between traps	358	336
II. Moving Upstream	**June 14 to July 28, 1951**	**Apr. 14 to May 18, 1952**
Estuarial trap up	310	636
Estuarial trap down	2	65
Estuarial trap up, then through stream trap up	124	160
Estuarial trap up, but not through stream trap up	184	411
Total stream trap up	247	464
Stream trap up, but recruited between traps	123	304

Data on movements of tagged trout into and out of the stream area between the two counting fences during specific periods are summarized in Table XII. The periods selected were not of equal length. However, they were periods during which major upstream and downstream movements occurred. They were also bounded before and after by a lull or cessation in movement of trout through the traps.

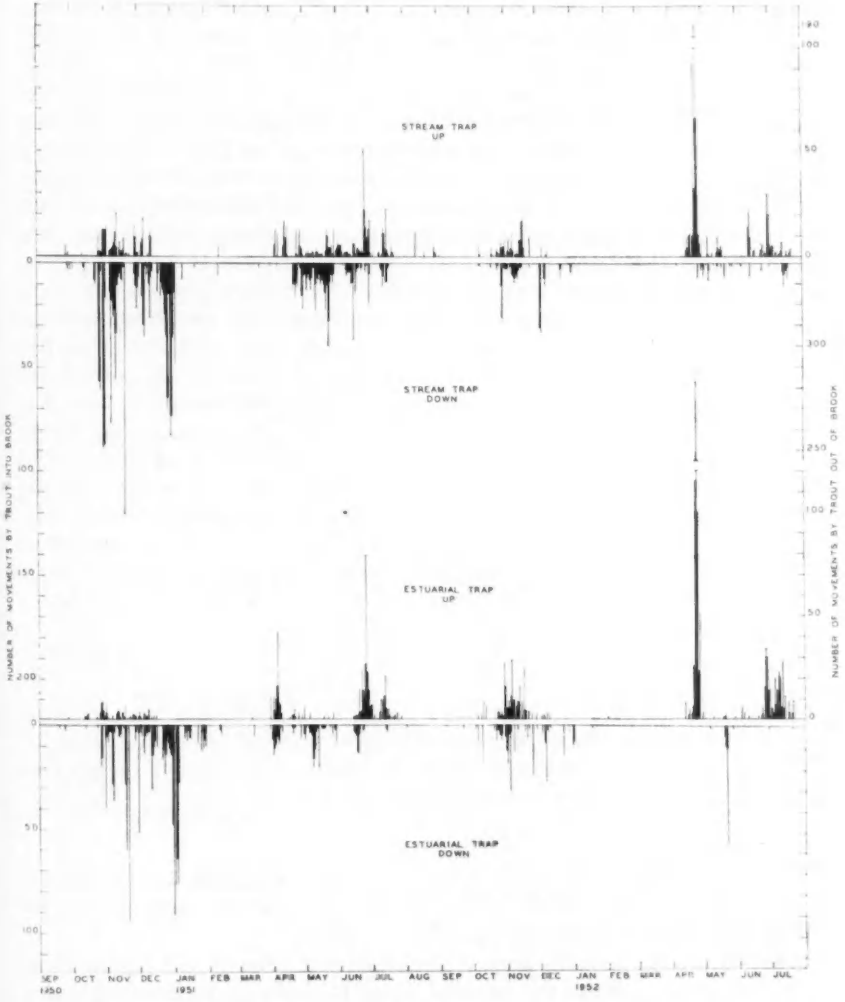

STREAM TRAP UP
STREAM TRAP DOWN
ESTUARIAL TRAP UP
ESTUARIAL TRAP DOWN
NUMBER OF MOVEMENTS BY TROUT INTO BROOK
NUMBER OF MOVEMENTS BY TROUT OUT OF BROOK
SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL
1950
1951
1952

FIG. 11. Movements of trout upstream and downstream through estuarial and stream traps. September, 1950, to July, 1952.

Only 48% in 1950 and 20% in 1951 of trout which came down through the stream trap in fall and early winter continued on their way to salt water during the same season. Relatively few reversed direction and moved up past the stream fence. Of trout which went through the estuarial trap to salt water, 32% in 1950 and 85% in 1951 came from the stream area between the fences. A large proportion (46% in 1950 and 73% in 1951) of the trout which came down through the stream trap remained in the lower parts of the brook. Subsequent records show that some of these trout either went to salt water or returned upstream during the next year. Of the 725 trout which moved down into, but did not leave the area between the fences in the fall and early winter period of 1950–51, there are records of 78 individuals going into salt water and 42 going back up through the stream trap on later dates, mainly in the spring and fall of 1951. Of the 220 tagged trout that remained between the fences during the fall–winter period 1951–52, the numbers subsequently running to salt water and upstream were 57 and 27 respectively. It is apparent that there was much movement by trout entirely within the fresh waters of the brook that trapping at the mouth of the stream could not disclose.

Movements between the two fences by ascending trout have also been analysed by tracing tagged individuals (Table XII). Two periods, June–July, 1951, and April–May, 1952, have been considered. Pattern of movements between fences was similar to that exhibited by descending trout. A large proportion (60% in 1951 and 65% in 1952) of trout which entered the brook did not proceed upstream out of the area between the fences during the periods in question. As with the descending trout, some moved out of the area at later dates. Again, however, the numbers which survived and were stimulated to do so constituted a minority (30 and 18 for the two years respectively). Of trout which went up through the stream trap during the two periods, 50% in 1951 and 66% in 1952 were recruited from the inter-fence part of the brook. Accordingly, at the same time that there were movements up through the estuarial trap, movements which began and terminated entirely within the fresh waters of the brook also occurred.

MOVEMENTS IN SALT WATER

White (1942) found at Moser River, Nova Scotia, that some trout moved 8 miles (13 km.) or more from their natal stream through salt water and ascended other streams. Aside from the observations by White, nothing has been reported concerning the extent of movements of brook trout in salt water.

In Ellerslie Estuary

We have, as previously noted, arbitrarily defined the limits of the Ellerslie Estuary at about 2¼ miles (3½ km.) seaward from the mouth of the brook (Fig. 1). Other smaller streams empty into the Ellerslie Estuary.

After descending into the estuary the majority of trout moved rapidly away from the immediate area of the estuarial fence. However, some from the spring runs into the estuary were found by seining to spend the summer months in tidal pools which were located about 100 yards (90 m.) below the fence. Trout from

spring runs continued to contribute to anglers' catches from these pools throughout the summer. The majority of trout which left the brook in spring and early summer, and later returned, did so within a time interval of 1 or 2 months (Table VIII). It seemed unlikely that many had journeyed sufficient distance to carry them out of the estuary. The accumulative evidence suggested strongly that a majority of the trout which left the brook in spring and early summer moved no farther than the estuary, and that good numbers stayed well to the head of it.

Information on trout which ran from the brook during fall and early winter was obtained from the commercial smelt fishery in the Ellerslie Estuary. In 1947 through February 1950 smelt fishermen reported capture of 324 tagged trout (tags were returned). Of these, 261 (81%) were captured during the same fall and winter period that they left the brook. The number of trout which ran from Ellerslie Brook during the fall and early winter periods from 1947 through 1950, and the number of those subsequently reported as taken in the smelt fishery, are presented in Table XIII. The data were biased by the increasing reluctance of smelt fishermen to report capture of tagged trout. Nevertheless, it is evident that the smelt fishery took a fair proportion of the trout which ran from the brook during the fall and winter periods. Time intervals between descent and subsequent recapture in the smelt fishery are given in Table XIV. These data show

TABLE XIII. Number of trout which ran from Ellerslie Brook in fall and winter months and number subsequently captured in estuarial smelt fishery.

Year and month		Number which left brook	Number captured in the smelt fishery	
		no.	*no.*	%
1947	September	42	5	12
	October	161	28	18
	November	482	39	8
	December	219	39	18
	January	126	0	0
1948	September	116	16	15
	October	150	12	8
	November	604	38	6
	December	550	16	3
	January	92	5	5
1949	September	63	3	5
	October	335	17	5
	November	262	10	4
	December	532	16	3
	January	30	0	0
1950	September	2	0	0
	October	80	4	5
	November	348	11	3
	December	361	1	0.3
	January	73	1	0.1
	Totals	4,628	261	6

TABLE XIV. Number of trout recaptured in estuarial smelt fishery at time intervals after descent through estuarial trap. Includes only those fish for which a definite date of recapture was known. Many trout captured in the smelt fishery were reported by season only.

Month through trap	Number of recaptures at various time intervals						
	Less than 1 week	1–2 weeks	2 weeks to 1 month	1–2 months	2–3 months	3–4 months	4–5 months
September	0	1	9	8	2	2	1
October	8	8	14	17	7	3	2
November	18	12	16	35	15	0	0
December	9	8	31	23	0	0	0

that trout which ran from the brook in fall and winter, and did not return to the brook within a short space of time, were still in the estuary until mid-February at least. Little movement might be expected at this time of year. In all likelihood the trout remained in the estuary until spring.

From Ellerslie Estuary

From April 1947 through January 1955, a total of 193 Ellerslie-tagged trout were reported angled outside the Ellerslie System. Places of recapture are indicated in Fig. 1. In the above period, 10,142 trout descended from Ellerslie Brook into the estuary. Although the records were incomplete, the small percentage (2%) of Ellerslie stock taken outside the system was undoubtedly indicative of a strong tendency by trout to stay in the home estuary after running to salt water.

With the exception of 11 fish, all trout captured outside the Ellerslie System were taken either in streams flowing into Malpeque Bay, or in inlets of the bay. Most returns were from Trout and Grand River Systems, the two nearest large streams to be encountered. Although quite comparable trout streams are to be found farther in a southeasterly direction around Malpeque Bay, only 1 recapture was reported from that region. Thus, those trout which left the Ellerslie Estuary appeared to move into the nearest large stream.

From Malpeque Bay

It is evident from recaptures (11) that few trout moved far from Malpeque Bay (Fig. 1). The most distant recapture was reported from Gaspereau River, Westmorland County, New Brunswick. This trout was at large for 15 months and had travelled a minimum distance of 200 miles (320 km.) after having been tagged at Ellerslie Brook. (This recapture is not indicated on Fig. 1.)

From Other Streams into Ellerslie

In addition to the tagging program carried on at Ellerslie Brook, 859 trout were tagged in 18 other Prince Edward Island streams in which trout were known to move between fresh and salt water. Subsequent to tagging, 47 trout (5.5%) were reported captured by anglers. All recaptures with one exception were made either in the stream of tagging or in neighbouring streams. The single exception was a trout which moved into Malpeque Bay from a stream about 15 miles

(24 km.) to the westward. Only one of the tagged trout moved into Ellerslie Brook. That individual was tagged in nearby Grant's Brook (Fig. 1).

Although fewer tags were used in the 18 outside streams than were in Ellerslie, the results of the two tagging programs were markedly similar. Few trout moved appreciable distances from the streams of tagging. The majority of those which did leave moved into nearby, and usually larger, streams. How many of the recaptures made in areas away from the home streams represented a permanent change of residence was not known. In two cases, tagged trout from Ellerslie Brook were captured by electrofishing in Trout River, released and subsequently recaptured again in Ellerslie. It is possible that a few trout moved into and out of a number of streams during their lifetime.

Reference to Table II shows that 5,031 untagged trout moved from salt water into Ellerslie Brook. Some were escapees from the brook. All evidence at hand suggests, however, that most of these trout were from nearby small streams which flow into the Ellerslie Estuary. Populations in some of these streams were found to consist largely of trout of age 0 and age 1. Essentially they were small nursery streams.

Available records show that in diminishing numbers trout moved from Ellerslie Brook, from Ellerslie Estuary and from Malpeque Bay into adjacent coastal waters of the Gulf of St. Lawrence.

SUMMARY OF MOVEMENTS

1. Movements of trout through traps in a counting fence near head of tide (estuarial fence) at Ellerslie Brook were recorded daily for 6 years. Similar records were also kept for 2 years at a second fence (stream fence) 650 yards upstream. All trout moving through the traps were jaw-tagged. Trout were also tagged in stream population studies. In total 16,165 trout were tagged.
2. Annual fluctuations occurred in both numbers of trout which moved through the traps and number of movements made by trout.
3. Movements between fresh and salt water were largely in the periods April-early July, and late September-early January. A similar pattern was noted in another Prince Edward Island stream. Prominent upstream movements were in April, June–July and November, and the downstream in May and in October to early January.
4. On some days different trout moved in both directions through the estuarial traps. At times movements were preponderantly in one direction; at other times movements involved large numbers of trout making simultaneous movements in both directions.
5. Trout captured in the estuarial traps were for the most part small (mean length 16.8 cm.) and young. Age 11 trout were in the majority. Few below 12 to 13 cm. were captured.
6. Ellerslie trout were short-lived. Consequently few trout survived sufficiently long to make repeated movements between fresh and salt water. Approximately half the trout which moved through the estuarial traps, in either direction, and later returned through the traps, did so within a month. The

closer the season of winter water temperatures the greater was the tendency for outward-moving trout to remain in salt water.

7. Short-distance movements, poorly detected at the counting fences, resulted in major population shifts in certain habitats of the stream in summer.
8. Movements through both counting fences were not always indicative of sustained movements by individuals for appreciable distances, either upstream or downstream.
9. The percentage of stream-reared trout which moved into salt water varied annually from 12% to 35%.
10. There was inconclusive evidence of an heritable propensity to sea-running.
11. After descending into salt water most trout appeared to remain in the estuary. The majority of those which left the estuary moved to neighbouring, and in most instances, larger streams. In diminishing numbers, trout left Ellerslie Brook, then Ellerslie Estuary. Few apparently left Malpeque Bay for the adjacent coastal waters.

MOVEMENTS IN RELATION TO ENVIRONMENTAL AND OTHER FACTORS

Water Level in the Brook

SUFFICIENT FLOW. On a few occasions in late summer the water level in Ellerslie Brook fell so low as to make it difficult for trout to pass certain riffles. Otherwise the water level was sufficiently high at all times to permit free passage of trout by all points on the brook.

HEIGHT OF WATER. The major movements of trout out of and into Ellerslie Brook occurred during the spring and fall seasons. These were seasons when the water was on the average at highest levels for the year. It is not to be implied that the trout moved between fresh and salt water only at the highest water levels. Reference to Figures 4, 5 and 6 shows that up- and downstream movements of trout at the estuarial fence were closely associated with rise and fall of the brook water level. Yet the numbers of trout which moved were only poorly correlated with the height of water reached during separate spates. At times, as many or more trout moved through the estuarial traps with a minor rise of water as with one that reached a decidedly higher level.

RISE AND FALL OF WATER. Trout largely moved with changing water levels in the brook. The relation between the degree of change and number of trout moving at the estuarial fence is illustrated in Fig. 12. The numbers of trout which moved from 1947 through 1952 in both directions for each ½-inch (13 mm.) change in water level, rising and falling, are shown. Changes in water level are based on a 24-hour period. The change in a specific 24-hour period was referable to the level, which may have been low or high, that obtained on the previous day. Records give the net change for the 24-hour period.

The majority of trout moved up- or downstream when changes in water level for the 24-hour periods were small (Fig. 12). The numbers of trout which moved with a rise in water level of 5 inches (13 cm.) or more are grouped together, and

thus at first glance assume undue importance. Trout moved by the estuarial fence with both rising and falling water, and when levels ranged from low to high. Capture at this one point, however, did not indicate the initial reaction of trout to changes in water level. However, since trout were caught in the estuarial traps while the water was still rising, it is apparent that some trout were stimulated

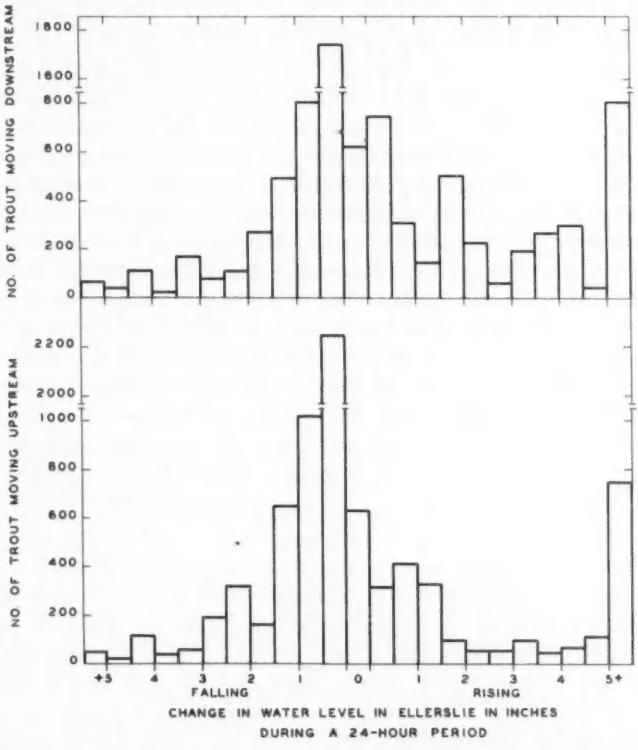


FIG. 12. Movements of trout through the estuarial traps in Ellerslie Brook in relation to changes in water level over 24-hour periods.

to move, and their movement sustained, with rising water. Capture on falling water could still indicate that movements started with increasing current and then continued on falling water. The data are not conclusive in showing that any trout taken in the estuarial traps began their movements on falling water. However, the short distances involved at Ellerslie Brook, and the continuance of movement over several days during periods of falling water, argue that movements which carried fish into the estuarial traps started in part on falling water and lessening current. The majority of trout were caught in the estuarial traps on falling water (Fig. 12).

MOVEMENTS IN ESTUARY IN RELATION TO CHANGING BROOK LEVELS. Trout which moved downstream into the estuarial traps at any one time were all subject to the changes in water level in the brook. Undoubtedly, those trout which were in the upper part of the estuary would also experience changes in water flow, but modified to a degree dependent upon the phase of tide. Proceeding seaward from the head of tide, direct effects of outflow from the brook would lessen. With a small rise of water at low levels, direct current effects in the estuary would soon be dampened or lost through tidal action. We are led to the view that when trout were moving upstream at the estuarial fence under these conditions, they had largely been in pools near the head of the estuary, and directly subjected to the small flow from the brook. Movement into the brook also occurred with moderate to heavy spates. Trout which were farther seaward in the estuary doubtless felt the effects of these. Following such spates, good numbers of trout have been observed in pools near the head of the estuary, but below the estuarial fence. These trout were then in position to feel quite fully the effects of subsequent spates, even if minor. For part of the trout at least, there appears to have been a succession of movements from the estuary with recurring spates that, by stages, resulted in their entrance into the brook. The time intervals between these stages of upstream movement, at least in the upper part of the estuary, may be quite lengthy. Some tagged trout which moved into pools near the head of tide in early summer were not observed to enter the brook until fall.

DIRECTION OF MOVEMENT AND CHANGING WATER LEVEL. Our discussion to this point has ignored the fact that trout moved *both upstream and downstream* through the estuarial traps with changing water levels in the brook. At times, movements were preponderantly, if not almost entirely, in one direction (Fig. 4, 5 and 6). On other occasions, trout moved both into and out of the brook on the same days, when in the vicinity of the estuarial fence they were all experiencing the same changes in water conditions. This latter situation obtained with trout of the same age and of comparable sizes. It is not surprising to have evidence of the individuality of trout and of random movements, or both, shown by reversal of direction of movement by some. Sometimes the same individuals were captured on successive days in the estuarial traps.

Elson (1939) studied the effects of current on movements of 4- to 6-centimetre brook trout in experimental troughs. Abrupt change from still water to current, and sudden increase in current and turbulence, increased the activity of the trout, and resulted usually in movement upstream. We have observed similar reactions by adult trout while draining experimental ponds. In the procedure trout were subjected to sudden increases in current from the relative stillness of a pond environment. With artificial freshets in Moser River, Nova Scotia, in 1942, Huntsman (1950) found that the number of brook trout which entered the river from salt water in summer was doubled over that in the three previous years without freshets. Approximation to these sudden changes was doubtless experienced at times by trout in Ellerslie Brook. For the most part, however, the changes in water level and current were much more gradual. Trout moved upstream in

Ellerslie Brook with such gradual changes. It is also the case that trout moved downstream under seemingly comparable current conditions. It would appear that the difference in direction of movement cannot be ascribed to current changes alone. Random movements were doubtless involved. Temperature of water, light, maturity are also factors, among others, that could affect the reactions of trout to current of a specific or varying velocity. Elson (1939) observed that, when temperature of the water was increased from 17 to 20°C., the reaction by trout to swim upstream with sudden increase in current did not materialize. "Rather the fish appeared to be weak and were swept to the lower end of the trough." Need for controlled behaviour studies in relation to water currents is obvious.

CHANGING WATER LEVEL WITHOUT MOVEMENTS BETWEEN FRESH AND SALT WATER. We have thus far considered the relationship between changing water levels in the brook and movements of trout only when they were captured at the estuarial fence. Figures 4, 5 and 6 illustrate that there were small to large changes in water level of the brook without accompanying captures. These latter occurrences were most commonly observed in late winter and early spring, and during midsummer. We have already seen that movements were made into and out of a pool in Ellerslie Brook in midsummer (Table XI). At least in 1951, appreciable changes in brook water level took place during the periods in question (Fig. 6). It is probable that trout reacted by moving with changes in current strength beyond a threshold value necessary to elicit reaction. Threshold values, and distance moved in response to stimulus from current once thresholds were reached, were doubtless conditioned by other factors.

Temperature of Water

LETHAL TEMPERATURE. The brook trout is a cool-water species. It is not customarily found in natural waters whose temperature appreciably exceeds 20°C. for extended periods. We have observed for New Brunswick lakes and streams, in common with Elson (1942), Baldwin (1948) and others for waters elsewhere, that brook trout move, if the opportunity permits, into cooler waters when the temperature approaches and rises above 20°C. The lethal temperature for the species varies according to the temperature to which the fish have previously become acclimated. Fry (1951) gives the "lethal temperature for prolonged exposure" as 25.3°C. for fully acclimated trout.

Water temperatures in Ellerslie Brook seldom approached lethal levels (Table I). High temperatures were encountered only for a few hours during the afternoons of isolated days, and then on the lower parts of the stream.

Maximum, minimum and mean summer temperatures of the bottom water in the estuary, at a point about 1 mile (1.6 km.) below the head of tide, are given in Table XV. Daily changes are graphed in Figures 3, 4, 5 and 6. Maximal temperatures in stream and estuary approximated each other. In the larger estuary, less directly affected by spring drainage and night cooling, temperature was held at higher levels for more extended periods. The open waters of Malpeque Bay

were somewhat cooler than the Ellerslie Estuary during the summer (Needler, 1931). Neither for stream nor estuary was there evidence that mortalities occurred from direct temperature effects.

TABLE XV. Temperature in degrees Centigrade for the bottom water of Ellerslie Estuary in summer. Records taken by the Fisheries Research Board's laboratory at Ellerslie.

	Maximum recorded			Minimum recorded			Mean			Mean at time of June to July run of trout into brook
	June	July	Aug.	June	July	Aug.	June	July	Aug.	
1946	21.6	22.2	22.2	12.6	17.8	16.8	16.5	19.7	20.0	19.2
1947	20.2	24.5	24.6	10.0	20.5	17.6	14.2	22.4	20.8	19.1
1948	20.7	23.3	22.8	9.3	18.0	19.8	15.8	20.9	21.1	20.0
1949	18.6	22.0	23.0	11.4	18.2	16.3	16.1	20.4	19.9	17.7
1950	18.8	21.3	21.6	13.2	16.6	18.7	16.4	19.4	20.3	20.5
1951	19.8	23.8	20.8	12.4	17.9	18.7	16.3	20.7	20.0	18.2
1952	17.8	23.8	23.3	12.3	17.0	18.5	14.9	20.0	21.5	19.9

TEMPERATURE SELECTION. Brook trout have been shown to select certain temperature levels when subjected to a temperature gradient under experimental conditions. At these levels the trout congregate and perform most efficiently, metabolically and in their responses to stimuli (Graham, 1949; Elson, 1942; Elson and Fisher, 1950; Sullivan, 1954). Level of selected or preferred temperature depends upon the temperature to which the trout have been acclimated. (We use "selected" and "preferred" as synonymous, only implying, as did Sullivan and Fisher (1953), what the fish is objectively observed to do.) With rising temperature trout select temperature levels somewhat higher than those to which they have been acclimated, until in the range from 14 to 19°C. selected and acclimation temperatures coincide (Fry, 1951). Such a temperature level has been termed the "final preferendum" by Fry (1947). With acclimation temperature above 19°C., trout select cooler water. However, the step-by-step relationship between acclimation and selected temperatures for brook trout is not always clear-cut. Sullivan and Fisher (1953) found a seemingly inherent seasonal change in early and late winter of selected temperature "which was distinct from the change in selected temperature brought about by changes of the acclimation temperature". Observed relationships between movements of trout and temperature of water at Ellerslie Brook are in many respects in harmony with the above experimental findings.

TEMPERATURE LEVEL. The number of movements by trout through the estuarial traps at various temperature levels in the stream are shown in Fig. 13. Appreciable movements occurred from 0 to 20°C., which was the range, except for short periods in summer, encountered in the brook. It was noteworthy that so many trout moved when the temperature of the water was at or approximated 0°C. (Supercooling, as indicated by the formation of frazil ice, occurred on numerous occasions in Ellerslie Brook; Smith and Saunders, 1956). However, movement largely ceased through the estuarial traps in winter after trout had been subjected to low temperature for some period of time.

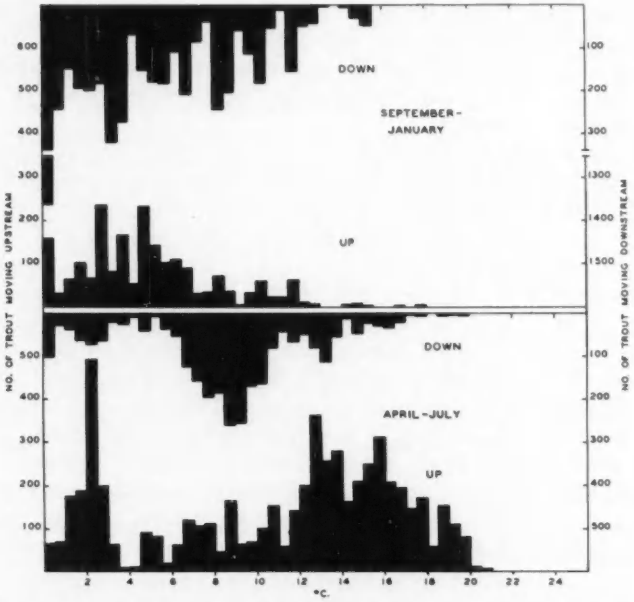


FIG. 13. Number of movements by trout through the estuarial traps on Ellerslie Brook at various temperature levels of the water in the stream.

TEMPERATURE GRADIENT. Most trout moved into and out of Ellerslie Brook in spring and early summer, and in fall and early winter. These were periods of the year when the steepest gradients in water temperature, both in stream and estuary, were encountered.

SPRING AND SUMMER MOVEMENTS. Large numbers of trout entered Ellerslie Brook in April (Fig. 4, 5 and 6). Major movements did not occur, however, until the brook temperature began to rise. Fig. 13 shows that the largest number of trout entered when the brook temperature reached 2°C. The estuary was colder than the stream at the time of these movements, but the difference was small. Although the estuary was ice-covered, or the ice in the process of break-up, the estuarial temperature was also rising under the influence of insolation and discharge from the brook (Needler, 1941). In this situation trout were moving from cold to somewhat warmer water.

As the season progressed through May both estuarial and brook temperatures rose, at first with little disparity between them, then with the former overreaching the latter (Fig. 4, 5, 6). Fluctuations occurred within and between years in both areas. In general, however, the temperature gradient was upward, with both acclimation and preferred temperatures increasing, probably in step with each other, except for possible seasonal discrepancies such as noted by Sullivan and Fisher (1953). It may be expected that under these rising temperature conditions

movements of trout would continue with environmental stimuli. There were movements of trout both into and out of Ellerslie Brook in May. They were predominantly out, in keeping with the attainment of higher temperatures in the estuary as the month progressed—temperatures which were below or in the level of final preferenda of trout.

On the other hand, in June and early July, just prior to and during strong inward movements at that season, the estuarial temperature remained quite consistently above that in the brook (Fig. 4, 5, 6). Trout were moving from warm to cooler water. Fry (1951) gives the temperature range of 14 to 19°C. as that of final preferenda for brook trout. When trout moved into Ellerslie Brook in June and July the mean bottom temperatures of the estuary were well up in or above this range (Table XV). At the same times the brook temperature approached or was within it (Table I). After entering the brook, trout made few movements sufficiently extensive to result in capture in the traps until fall. Field and experimental observations were accordingly in agreement that the trout remained relatively quiescent at a temperature of final preferendum in the brook.

Trout were observed in the estuary during the summer. Although summer temperatures in the estuary were not as suitable for trout as those in the brook, they were not intolerably high. Apparently temperatures did not reach such persistent high levels in summer as to result in a movement of all trout from the estuary.

Trout in the estuary had two opportunities to move into cooler water when temperatures approached summer maximal values. One opportunity was Ellerslie Brook. The other was the open waters of Malpeque Bay, where temperatures were somewhat below those in the estuary (Needler, 1931), but not as low as in the brook. One may speculate that those trout which left the Ellerslie System, as shown by capture of Ellerslie-tagged trout in outside streams, did so at this season. We have records to show that trout which left Ellerslie Brook in late spring were captured during the summer of the same year in outside streams.

White (1940, 1941) reported movements of trout into Moser River, Nova Scotia, in summer, principally in July. The morning temperature of Moser River when trout were entering in July 1941 was about 18–20°C., with maximal afternoon levels to 26°C. (Day and Wilder, 1941). Contemporary water temperatures for the Moser Estuary and contiguous coast are not available, but presumably those for the coastal waters would be cooler than those given above for the river. If trout were moving from these waters into the estuary and river, then temperature conditions were opposite to what obtained at Ellerslie Brook during the inward June–July movements. However, comparison of the situations at Ellerslie Brook and Moser River do not appear feasible without more data on the location of the trout and the environmental conditions that obtained there.

FALL AND WINTER MOVEMENTS. Significant movements through the estuarial traps at Ellerslie Brook did not occur in fall until brook and estuarial temperature fell below the level of final preferenda (14 to 19°C.) (Fig. 13). However, the estuary cooled more slowly than the brook. Probably estuary and brook temperatures were about the same when in and out movements first started. In any

case fall movements continued with declining water temperature until early January by which time, in both stream and estuary, trout had been exposed to 0°C. for appreciable periods. With declining water temperature, preferred temperatures were realized by trout only temporarily if at all. Sufficient exposure to the winter temperature level, with metabolism reduced to a minimum, apparently terminated movements into and out of the brook. In spring, with trout having been in cold water for the winter, movement did not materialize until the temperature rose above 0°C. In fall, on the other hand, there was a time lag after 0°C. was reached before movements stopped between fresh and salt water. (The periods between 0°C. readings in the brook and cessation in early winter of movements through the estuarial traps varied somewhat between years to a maximum of about one month.) With decreasing temperature, rate of metabolism and rate of acclimation are reduced (Brett, 1956). Full acclimation at low temperatures is not realized for days or weeks. The time lag before observable movement ceased (or began in the spring) at Ellerslie Brook appeared associated with a slow rate of acclimation at low temperatures.

ABERRANT MOVEMENTS. Numbers of trout moved from Ellerslie Brook on three occasions when relationship of temperature to movements remained obscure. One in mid-February 1948, occurred during mild weather, but without a rise in water temperature, at least on the lower part of the brook. Movements in March 1949 coincided with the opening of the brook, increased water levels, yet only a tenth or two of a degree rise in water temperature. A third movement on April 15, 1950 involved 72 trout without sufficient temperature changes in water for our instrument to record them. However, frazil ice formed in the brook at this time.

INTERACTION OF TEMPERATURE AND CHANGING WATER LEVEL. Movements of trout into and out of Ellerslie Brook were closely associated with changes in stream water level. The association was so close that in our observations there appeared no clear-cut instances when trout moved in numbers through the estuarial traps without changes, albeit at times small, in flow of water. However, it has been noted that even marked changes in water level in Ellerslie Brook were not always accompanied by movements into and out of salt water. Such occurred in summer, winter and early spring. These were periods when in relation to temperature of water trout were least disposed to move, that is from temperatures of final preferenda and after acclimation to the cold waters of winter. Thus, for most movements in Ellerslie Brook, and probably in the upper reaches of the estuary as well, it would appear that temperature conditioned trout to move and change in current provided the stimulus for them to do so. This explanation is doubtless over-simple for all movements within or between fresh and salt water at Ellerslie Brook. In the estuary, currents resulting from spates in the brook would vary in intensity with distance from the stream mouth, to be ultimately dissipated by tidal changes. However, gradients in temperature and salinity would be more persistent at these distances. Our data do not clearly show that temperature change, or level, directly initiated movements of trout. (This has been

thoroughly discussed by Sullivan, 1954.) On the other hand interaction of temperature with current changes and no doubt with other factors as well, appeared potent in this respect.

DIRECTED MOVEMENTS. Changes in water current and temperature gradients leading to selection of temperature preferenda, would seemingly be directive factors in movements of trout at Ellerslie Brook. Movements predominantly in one direction seem to be best explained by the directive influences of such factors, separately or through their interaction. Under her experimental conditions, Sullivan (1954) observed that "trout show no tendency to orient in any particular way to the temperature gradient, nor could any evidence be gathered to show that trout make more movements toward any particular temperature region than toward others". However, she points out "that fish must move when they select temperature and that their movements must be modified by the temperatures encountered". Many movements into the traps at Ellerslie Brook were doubtless random in nature. Recapture of trout within short intervals of time argue for this viewpoint. By random movements alone, temperature selection could be realized. However, there were other movements by trout through the traps that were apparently directed. A good example was the upstream movements in April 1952 (Fig. 6). These movements through the estuarial and stream traps have been analysed (Table XII). Some trout terminated their movements for the time being in the section of the stream between traps, while others started their movements in the same area. Nonetheless, capture in the traps showed that practically all movements were consistently upstream. This occurred although movements by trout which were taken in both the estuarial and stream traps were interrupted up to 24 hours by retention in the traps. Movements occurred with changes in temperature and flow of water. These factors seemed dominant in their influence, although in the complexity of the natural environment of Ellerslie Brook, one cannot ignore the influence of others.

LIGHT

Sullivan and Fisher (1954) found under experimental conditions that when the selected temperature region of a temperature gradient was strongly illuminated (artificially) it was rarely entered by trout which had darker areas available to them. For lower light intensities, however, they concluded that "it was the response to temperature which prevailed and in spite of the illumination the organisms selected temperatures in a normal way". There is general agreement between these experimental observations and those that occurred in the field at Ellerslie Brook.

The majority of trout moved into the Ellerslie traps at night (Table XVI). Elson (1938) reports similar observations made at a trap on Trout Brook, Nova Scotia. The small number of movements during the day was associated, with few exceptions, with cloudy skies, rain or both. These conditions were usually inseparable from changing water levels. However, it is clear that, notwithstanding the dominant effects of temperature and changing current on movements of trout, light had an overriding influence when movements were under way, sufficient to make them largely nocturnal.

TABLE XVI. Movements of trout upstream through the estuarial trap, May 12–20 and June 4–July 2, 1954, at different periods of day and night.

	8 a.m. to 6 p.m.	6 to 10 p.m.	10 p.m. to 2 a.m.	2 to 8 a.m.
Number of movements	65	264	198	150
Number of hours	380	152	152	228
Number of movements per hour	0.2	1.7	1.3	0.8

TURBIDITY

The "red" soil of Prince Edward Island is easily eroded. Ellerslie Brook becomes turbid with each rain, but to a varying degree dependent upon rate and amount of precipitation. Trout moved into and out of Ellerslie Brook in large numbers with both small and large changes in water level, and thus with from relatively clear to highly turbid water. Turbidity in any possible effects upon movements of trout was intimately associated with changing water levels, but from what we could observe appeared to have a minor influence.

SALINITY

Huntsman (1951) in reference to occurrence of brook trout in salt water writes: "The shore waters where they are found is not of very high salinity. Where salinity is very high, as along the shores of the Bay of Fundy, they are not found in the sea". Bailey *et al.* (1954) give the normal annual range of salinity in the Bay of Fundy as 31.1 to 32.5‰ for surface and 31.9 to 32.8‰ for bottom waters.

Wilder (1952) attempted to determine resistance of brook trout to running salt water (30‰). No acclimation to any salinity was attempted. He found that the resistance of immature trout increased with size. This relationship did not hold as well for larger, ripe trout. Wilder's data show that relatively few trout below 10 cm. survived for any appreciable length of time when directly transferred from fresh water into water of the above salinity. Few trout below this size were known to have moved into the Ellerslie Estuary (Fig. 8 and 9).

In reference to salinities in Malpeque Bay, Needler (1931) writes: "There is very little difference between the salinity of the surface and the bottom water in the bay or in the inlets, except at the heads of the latter for short periods after heavy rains". Salinity records held at the Biological Station, St. Andrews, show that salinities of the waters of Malpeque Bay, and of the adjacent coastal areas are, with the exception of the summer months, markedly similar. In summer, salinities are higher in the bay. Annual range in both areas is from 26 to 31‰.

It is clear from the preceding discussion that trout which ran into the Ellerslie estuary encountered relatively high salinities a short distance below the estuarial fence. We have shown that trout spent the winter, or the greater part of it, in the estuary. Some trout moved through the estuary into the open bay. Since salinities were almost the same throughout Malpeque Bay we need not consider salinity as a barrier in their subsequent movements around the bay or into the coastal waters.

The relation of salinity to the movements of trout of age 0 will be discussed below.

Tides

Tide records have been kept at the Ellerslie estuarial fence. No relationship was found at this point between tides and movements of trout either into or out of the brook. Trout largely entered the traps at night regardless of the phase of tide. White (1930) observes for trout in Prince Edward Island waters that "the sea-run trout may run into the estuaries with the flood tides and return to the deeper water with the ebbing tides. When following the tides in the estuaries we have found them travelling in shoals". Movements in relation to tides may have occurred in the Ellerslie Estuary. However, our observations were confined to the immediate area of the estuarial fence.

Living Space

That space factors are important in the growth of fish has been shown by Brown (1957). Huntsman (1950) postulates that crowding of brook trout in streams is a factor in sea-running. In a previous paper we concluded that availability of suitable hiding places was a dominant factor in delimiting the carrying capacity of a small stream, tributary to Ellerslie Brook, for trout older than age 0 (Saunders and Smith, 1955).

We believe that living space was an important underlying factor in the running of Ellerslie-reared trout to salt water at ages I and II. If this thesis is correct, then crowding of the trout was not too serious, as shown by the small proportion of stream-reared fish which ran to salt water (Table IX, Fig. 10). It is pertinent, as we have already noted, that when a pond was formed between the stream and salt water most trout moved no farther than the pond.

Maturity

There was no indication that brook trout fingerlings (age 0) ran into salt water at Ellerslie Brook. Possibly numbers were swept unobserved from the brook during the heavier freshets. However, only an occasional individual was captured in the estuarial traps or observed in their vicinity. None was taken in the fall of 1947 when the traps were lined with fine-mesh wire adequate to retain fingerlings. The inter-tidal zone at Ellerslie Brook was physically a poor habitat for trout fingerlings. This zone is open, with muddy bottom, quite different from the riffle areas in the stream where fingerlings were consistently encountered.

Wilder (1952) killed fingerling brook trout from coastal streams of New Brunswick by transferring them directly from fresh to salt water (30‰). Tolerance limits for acclimated fingerlings to salinity levels that could be encountered in Ellerslie Estuary (up to 29‰) are apparently unknown. Fingerlings may react to avoid salinities which might be lethal. This assumes that fingerlings in their movements encounter salt water. Fin-clipping showed, to the contrary, that most fingerlings in Ellerslie Brook did not make sufficiently extensive movement to do so. Establishment of "homes" appeared to be strongly developed by these fish.

A good proportion of the trout in all movements through the estuarial traps consisted of immature yearlings. It would hardly seem justified to designate any movements between fresh and salt water as spawning runs. A majority of the

largest trout (most likely to spawn that year) which entered Ellerslie Brook were encountered in June and early July (Fig. 8). Mature trout in less proportions also entered during fall. As with the other major movements during the year, those in fall were closely associated with changes in environmental factors that appeared conducive to movements. That fall upstream movements occurred just prior to and during the spawning period seems to be the only basis to suggest that they were spawning runs, and that maturity was a factor in their occurrence at that particular season.

Once on spawning areas, however, then reactions associated with maturation and spawning might override effects of environmental stimuli that at other times would result in movements of trout to salt water. It is obvious that such reactions were not entirely effective since larger mature trout continued to move out of and into Ellerslie Brook during the entire fall period (Fig. 8, 9, 14). Ripe females and males were taken moving out at the estuarial fence.

In Fig. 14 length frequencies among the trout which moved out of Ellerslie Brook in the fall of 1946 are plotted for three periods, September–October, November, December–January. The length frequencies have been separated at 17 centimetres, which is approximately the mean length of age II trout (Table V). The division roughly separates non-spawners from spawners, although precocious male yearlings were observed. If maturation and spawning were factors in dampening effects of others that would usually occasion movements, then it could be expected that the late outward movements, after or near the close of the spawning period, would contain the highest proportion of large trout. As seen in Figure 14 this was the situation. We have interpreted these data as showing effects of maturity on movements of trout, but only to a demonstrable degree at spawning time, and when they were on or near the spawning beds.

White (1940) recognized brook trout smolts in his studies at Moser River, Nova Scotia. Silvering (guanin coating) was associated with movements of trout to salt water for the first time. We were not able to recognize trout smolts at Ellerslie Brook. However, a coating of guanin was acquired by the Ellerslie trout after a sojourn in salt water, as is typically the case for sea-running brook trout generally. Physiological changes involved in silvering, or at least to the point of silvering being manifested, were not a prerequisite to the movement of Ellerslie trout to salt water.

Trapping and Other Capture Procedures

To some extent the counting fences on Ellerslie Brook interfered with movements of trout. This interference was minor when factors which conditioned movements of trout were operating most strongly. At other times, such as during the summer months, trout have been observed to spend long periods in pools just below the estuarial fence or in the immediate area of the stream fence. This occurred although the entrances to traps were only a few feet away. However, we have no reason to believe that the pattern of movements of trout in Ellerslie Brook would have been substantially different without the counting fences.

Handling and detention of trout in traps had no apparent effect, unless temporary, on their subsequent movements. That trout continued their interrupted movements in either direction has been shown by their recapture in one fence after having been tagged and released at the other.

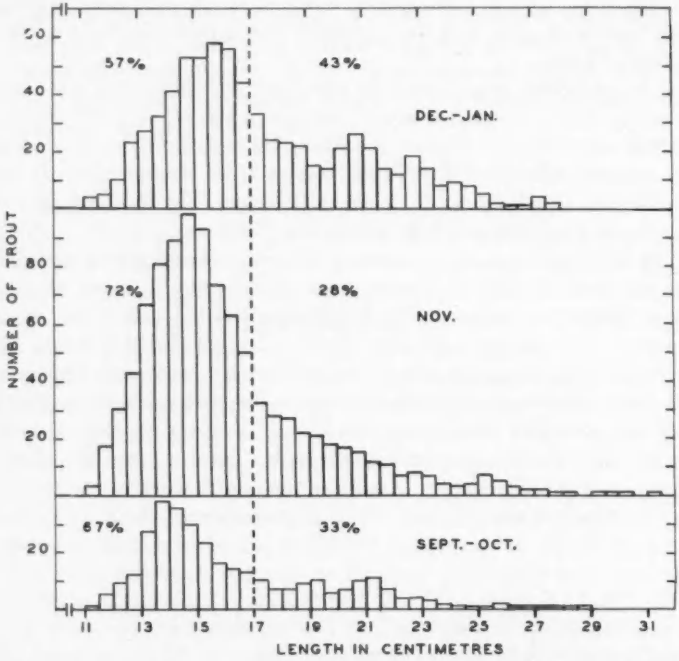


FIG. 14. Length frequencies of trout which moved out of Ellerslie Brook in the fall of 1946. The vertical broken line roughly separates immature and mature trout.

Trout were also tagged during the annual summer assessments of the population of Ellerslie Brook. Prior to 1951 trout were captured by seining. In 1951 they were electrofished. If seining and electrofishing had subsequent effects on behaviour of the trout we were not aware of them. Trout captured by both methods later moved to salt water in similar proportions.

SUMMARY OF MOVEMENTS IN RELATION TO ENVIRONMENTAL AND OTHER FACTORS

1. Movements of trout between fresh and salt water were very closely associated with rise and fall of water level in Ellerslie Brook. Numbers of trout which moved were not correlated in a direct manner with height of water. Trout

moved with both rising and falling water when levels ranged from low to high.

2. Trout in the lower part of the estuary appeared to reach the brook by a succession of movements with recurring spates.
3. Appreciable movements of trout between fresh and salt water occurred when the brook temperature was from 0 to 20°C. Movements in spring and early summer were into preferred temperatures. Few trout moved between fresh and salt water in winter after becoming acclimated to 0°C., or in summer when water of the brook was at a temperature of final preferenda (14 to 19°C.), although marked changes in water level occurred.
4. Trout moved for some time after water reached 0°C. Continuance of movements in water of 0°C. seemed associated with slow rate of acclimation with falling and low temperatures.
5. Movements between fresh and salt water were both random and directed.
6. For most movements it appeared that temperature conditioned the trout to move and change in current provided the stimulus.
7. Light acted to make the movements largely nocturnal.
8. Such factors as turbidity, salinity and tides did not have demonstrable influences on movements of trout between fresh and salt water.
9. Suitable living space was considered an important underlying factor in the running of Ellerslie-reared trout to salt water.
10. On the spawning ground reactions associated with maturation and spawning seemed to override effects of other stimuli that at other times would result in movements of trout to salt water.
11. There was no reason to believe that the pattern of movements of trout at Ellerslie Brook would have been substantially different without counting fences.

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On the Occurrence and Distribution of Larval Herring (*Clupea harengus* L.) in the Bay of Fundy and the Gulf of Maine[1,2]

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ABSTRACT

A major portion of the Bay of Fundy and Gulf of Maine has been surveyed for occurrence and distribution of herring larvae. Plankton samples obtained with Hardy continuous plankton recorders and plankton nets confirm major spawning areas off the southwest coast of Nova Scotia and on the northern edge of Georges Bank. Newly hatched larvae were found in abundance in these areas, but nowhere else. Drift of larvae as indicated by non-tidal surface currents suggests that Nova Scotia spawnings may contribute substantially to commercial stocks of herring in inshore areas of Maine and New Brunswick. It is possible that Georges Bank spawnings also supply herring to this region.

INTRODUCTION

Canada and the United States have a common interest in a fishery for young herring that are found in vast numbers in inshore waters of Charlotte County, New Brunswick, and along the Maine coast. Average annual landings approximate 200 million pounds and provide raw material for "sardine" canneries, pet food, and reduction plants.

There has been no recent evidence of major spawnings within the principal coastal "sardine" areas; in fact during the past 10 years only small quantities of adult herring have been caught there. About 1875, when the "sardine" industry started to become important, the fishery for adult herring in the area began to decline, and this trend has continued (Huntsman, 1953). Spawnings at Grand Manan, New Brunswick, and along the Maine coast were very extensive at one time (Earle, 1887) and still occur fairly regularly but are of only minor importance. Where then are the breeding grounds and the nursery areas for the fish that populate the region? What is the survival, growth, and dispersal of larvae and how are they transported?

To answer these questions, the Fisheries Research Board of Canada and the United States Fish and Wildlife Service began, in 1956, a co-operative investigation of the offshore areas of the Bay of Fundy and the Gulf of Maine.

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[2]This paper is based on investigations carried on jointly by the Fisheries Research Board of Canada and the U.S. Fish and Wildlife Service.

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The main part of the program was carried on from September through February in 1956–57 and 1957–58. Additional data were available from *Prince* station tows taken monthly in the Passamaquoddy region and from cruises made by the M. V. *T. N. Gill* from May 1955 to January 1956. In March 1958, cruises with the M. V. *Mallotus* were carried out in the Grand Manan area at the entrance to the Bay of Fundy, and in St. Mary Bay, Nova Scotia.

Autumn and winter months were selected for the co-operative cruises because of known spawnings in southwestern Nova Scotia and on Georges Bank in August and September. Surveys were designed to study the abundance, size and distribution of the larvae that resulted from these spawnings.

Although the problem of the origin of the "sardine" herring in southern New Brunswick and Maine remains unsolved, some progress has been made and the discoveries to date are recorded in the following preliminary report.

MATERIALS AND METHODS

Canadian vessels used were M. V. *Harengus* (Fig. 1), C. N. A. V. *Fort Frances*, M. B. *Mallotus*, and M. V. *J. J. Cowie*. United States Fish and Wildlife Service supplied the M. V. *Silver Bay* (Fig. 1), M. V. *Albatross III*, M. V. *Delaware*, and M. V. *T. N. Gill*. In the initial planning, a series of cruise lines and stations was established (Fig. 2) which were followed as closely as possible throughout the investigation. The total length of the cruise lines was approximately 2,550 miles. Hardy continuous plankton recorders were towed throughout the cruises. Recorders had an aperture ¾ inch. (19 mm.) square and propeller angle setting of 70°. This propeller setting usually provided a 2-inch (51 mm.) section of gauze for each 5 miles (8 km.) of cruising. Canadian vessels towed one recorder at a depth of 10 metres. United States vessels used 2 recorders—one at the surface and one at 10 metres.

Additional plankton collections were made with silk or nylon 1-metre plankton nets of #0 mesh (12–15 threads per cm.). Nets were towed for 15 minutes at each station at approximately 3 knots. Two kinds of 3-level tows were made. One was at 0, 5, and 10 metres and the other was at 0, 10, and 20 metres. Tows in the September 1956 to February 1957 cruises were of the first type; in the September to November 1957 cruises of the *Harengus*, the second type was used. United States vessels made plankton tows every 4 hours and Canadian vessels towed at 95 established stations that were about 4 hours steaming-time apart.

Herring larvae were removed from the recorder gauzes and plankton collections. In tows that contained more than 100 larvae, a sample of 100 was taken for length measurements, otherwise all larvae were measured. Two length measurements were used, viz., *total length* from tip of lower jaw to longer lobe of caudal fin and *standard length* from tip of lower jaw to caudal peduncle. For this report, standard lengths of larvae 12 mm. and larger were converted to total lengths by use of the formula:

$$Y\,(\text{total length}) = 1.181X(\text{standard length}) - 2.0$$

Below 12 mm. the two lengths are identical.

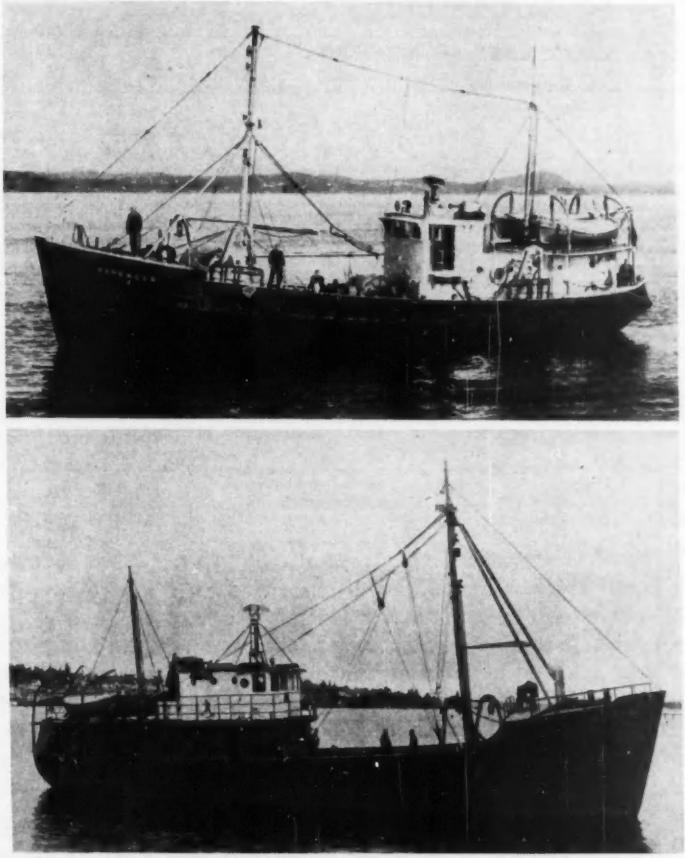

FIG. 1. Two of the vessels used for the plankton cruises (upper) Canadian research vessel M. V. *Harengus*, (lower) United States chartered vessel M. V. *Silver Bay*.

Occurrence of herring larvae at two plankton stations in the Passamaquoddy region, *Prince* 5 (Lat. 44° 57′ 10″ N, Long. 66° 51′ 00″ W) and *Prince* 6 (Lat. 45° 04′ 54″ N. Long. 67° 06′ 07″ W) was recorded. These stations have been occupied monthly for more than 20 years by the Fisheries Research Board of Canada's St. Andrews Biological Station, giving 901 *Prince* Station collections, covering the years 1942 to 1958 (March) for *Prince* 5 and 1946 to 1958 (March) for *Prince* 6. Routine at *Prince* stations included vertical tows from 90 to 0 metres, and 15-minute oblique tows, one from 23 to 18 metres and the other from 7 to 5 metres. All tows were made with a 1-metre #0 plankton net.

From May 1955 to January 1956, 10 plankton cruises using the United States research vessel *T. N. Gill* were made chiefly in coastal waters of the Gulf of

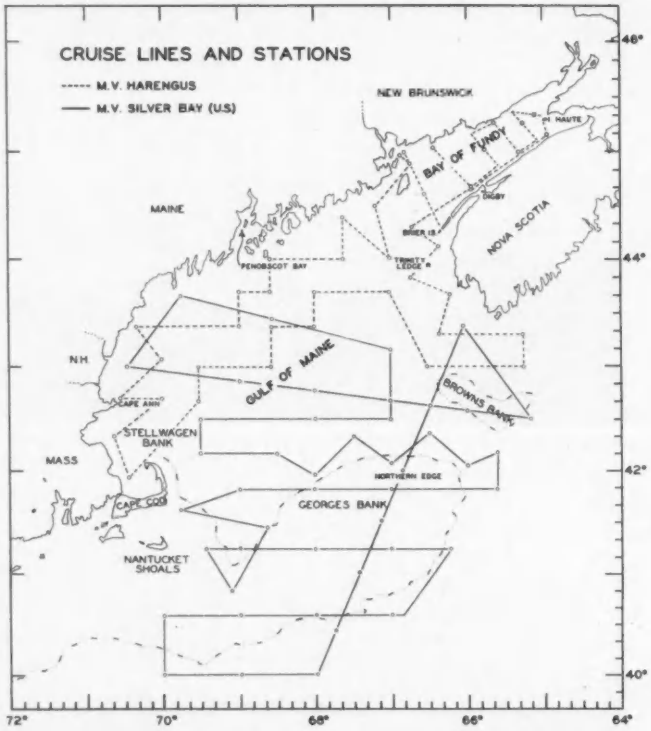

FIG. 2. Cruise lines and stations occupied during the September to February cruises 1956–57 and 1957–58.

Maine. A total of 191 plankton tows was taken with a 1-metre net towed for 15 minutes at 0, 5, and 10 metres (5 minutes at each depth). Data on larvae taken are included in this report.

During most cruises, bathythermograph casts, drift bottle releases, and air and surface water temperature observations were taken.

ABUNDANCE OF HERRING LARVAE

The total number of herring larvae examined was 50,037. The numbers of larvae taken, the gear used, the numbers of 1-metre net tows made, and the distances Hardy recorders were towed are listed in Table I. There were 30 larvae taken at *Prince* stations and 353 during *T. N. Gill* cruises. The majority of larvae, however, were taken in the joint cruises from September to February 1956–57 and 1957–58. Except for December 1956, when additional tows were made in areas where larvae were known to be abundant, largest numbers were taken in September and October of each year (Table I). The catch decreased sharply

TABLE I. Herring larvae caught in different years.

Date	Vessel or Station	1-metre net Larvae	1-metre net Tows	Hardy recorder Larvae	Hardy recorder Miles towed
		no.	*no.*	*no.*	*no.*
1942-1957	*Prince* Station 5	23	487	...	...
1946-1957	*Prince* Station 6	7	414	...	...
1955-1956	*T. N. Gill*	325	191	28	3,051
Sept. 1956	*Silver Bay, Harengus*	5,619	101	23	2,619
Oct. 1956	*Silver Bay, Harengus*	6,453	96	52	2,788
Nov. 1956	*Silver Bay, Harengus*	1,635	100	37	2,768
Dec. 1956	*Silver Bay*	18,319	109	...	...
Jan. 1957	*Delaware*	196	51	9	1,842
Feb. 1957	*Albatross III*	259	97	18	1,550
Sept. 1957	*Harengus*	4,187	53	0	1,345
Oct. 1957	*Harengus*	12,017	70	1	615
Nov. 1957	*Harengus*	347	48	11	510
Dec. 1957	*Albatross III, Delaware*	271	76	34	2,347
Jan. 1958	*Albatross III, Delaware*	93	62	23	1,804
Feb. 1958	*Fort Francis*	46	67	4	1,795
	Total	49,797	2,022	240	23,034

in November and was very light in January and February. Additional tows in December 1956 were made to investigate depth distribution of larvae and these account, in part, for the large number (18,319) taken during that month.

No attempt has been made here to compare abundance of larvae for the two seasons 1956–57 and 1957–58 because of variations in numbers of tows and in localities where tows were made. In both seasons, large numbers of larvae were taken in a few tows and a comparison of average numbers per tow would have little meaning. Only 240 larvae were taken with plankton recorders, in contrast to 49,797 in 1-metre nets.

DISTRIBUTION OF HERRING LARVAE

Catches indicate that during September larvae are not widely dispersed in the Gulf of Maine. In September 1956 (Fig. 3A) large concentrations were found on Georges Bank. Small numbers were found around Nantucket Shoals off Massachusetts and near Ile Haute and Brier Island in the Bay of Fundy. A few individuals were taken off the coast of Maine. In September 1957 (Fig. 3B) cruises covered only the Bay of Fundy, the coast of Maine and the northern edge of Georges Bank. The only herring larvae captured were in the Bay of Fundy and along the southwest coast of Nova Scotia. A major concentration occurred near Brier Island. Absence of larvae on Georges Bank suggests that herring in the area had not spawned, or eggs had not yet hatched.

In October, larvae were more widely distributed. In October 1956 (Fig. 3C), larvae occurred throughout most of the Georges Bank area with major concentrations on the northern edge. Both Hardy recorder and plankton net samples caught larvae in the southern portion of Georges Bank. Scattered larvae were

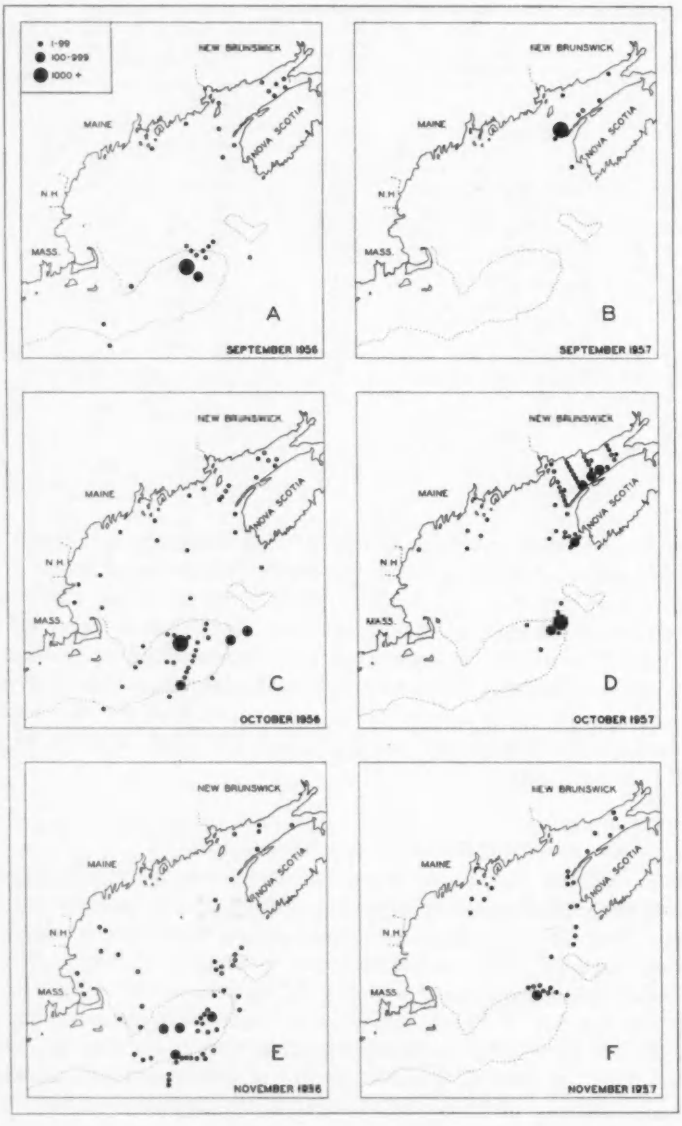

FIG. 3. Distribution of herring larvae September to November 1956 and 1957.

taken in the Bay of Fundy. A few were found around Stellwagen Bank and offshore from Penobscot Bay. In October 1957 (Fig. 3D), large numbers were taken on the northern edge of Georges Bank and near Trinity Ledges at the southern tip of Nova Scotia. Larvae were taken in 29 out of 33 tows in the Bay of Fundy. They were well dispersed throughout the Bay with largest concentrations near Digby. Some larvae were taken offshore in the vicinity of Penobscot Bay and off Cape Cod.

Larvae in November 1956 (Fig. 3E) were more widely dispersed than for most months during the survey. They were heavily concentrated on Georges Bank but, in general, were farther south than in September and October. Concentrations on the northern edge of Georges Bank in September and October appear to have been broken up with some larvae having moved northeast over Browns Bank, while the majority had moved south on Georges Bank. Only a few larvae were caught in the Bay of Fundy, along the Maine coast, on Stellwagen Bank and in the middle of the Gulf of Maine. In November 1957 (Fig. 3F), larvae were again concentrated heavily on the northern edge of Georges Bank. As in November 1956, some dispersal of larvae northward toward the Nova Scotia coast was evident, while in the Bay of Fundy major concentrations were no longer evident, and small concentrations were found in the northern part of the Bay and along the west coast of Nova Scotia. Along the Maine coast, a few larvae were taken offshore in the vicinity of Penobscot Bay.

In December 1956 (Fig. 4A), sampling was restricted to Georges Bank and inshore areas of Maine and New Hampshire. Heavy concentrations of larvae were found on the southern half of Georges Bank and smaller concentrations on Stellwagen Bank. In December 1957 (Fig. 4B), larvae from 1-metre net catches were scarce over Georges Bank and in the Bay of Fundy. The heavy concentrations of September, October, and November now showed a more widely dispersed pattern of distribution.

In January 1957 and 1958 (Fig. 4C, and D), distributions were similar for the Gulf of Maine and Georges Bank. There was no cruise in the Bay of Fundy in January 1957. In January 1958, small concentrations of larvae were found at more than half (12 out of 22) of the stations occupied.

In February 1957, sampling was restricted to inshore areas of the Gulf of Maine and the Bay of Fundy and a wide distribution of larvae was observed as shown in Fig. 4E. In February 1958 (Fig. 4F), only small numbers were taken anywhere, most of them on or immediately north of Georges Bank.

Differences between catches in January and February of both years were chiefly in numbers taken rather than distribution. It is likely that by January the larvae were large enough to avoid the plankton nets.

Distribution and numbers of larvae taken during *T. N. Gill* cruises are shown in Fig. 5. In April, 17 larvae were caught west of Penobscot Bay, Maine. In June and July, no larvae were taken. In August, 18 newly hatched larvae were taken in one tow on Trinity Ledges. In October no larvae were taken in a cruise from Penobscot Bay to Cape Ann. A November cruise in the Gulf of Maine, on Georges Bank, and in the Bay of Fundy took 51 larvae on Georges and

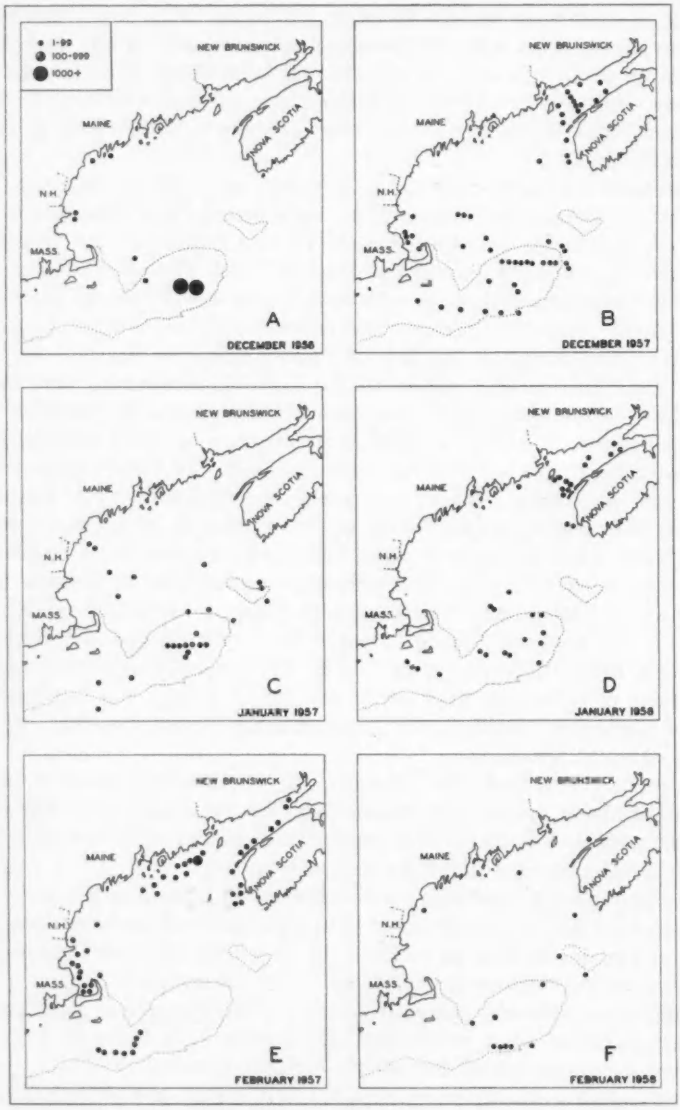

FIG. 4. Distribution of herring larvae December to February 1956–57 and 1957–58.

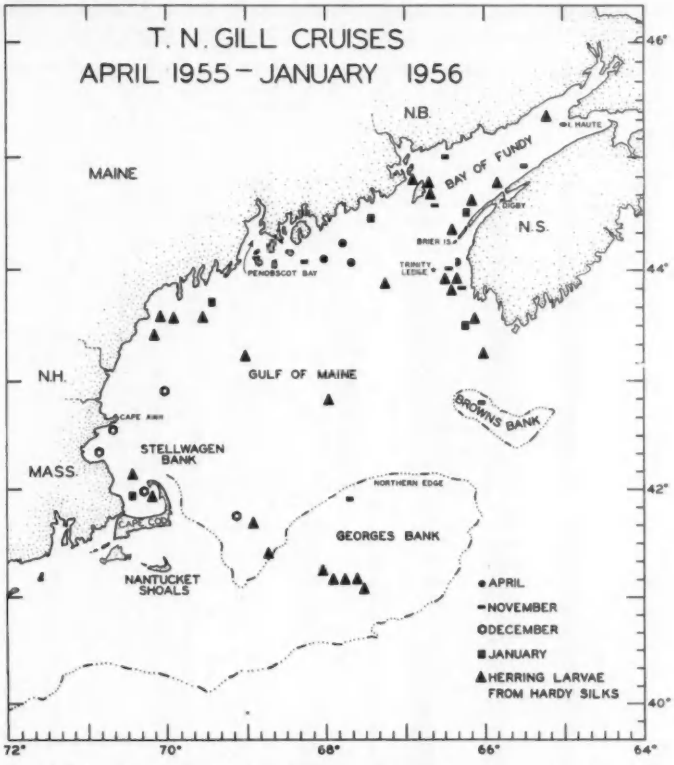

FIG. 5. Distribution of herring larvae caught during the *T. N. Gill* cruises April 1955 to January 1956.

Browns Banks, on Trinity Ledges, in the Bay of Fundy, and around Penobscot Bay. In December, a short cruise was made along the New England coast during which 187 larvae were taken. Fifty-two herring larvae were taken during a January cruise along the western coast of Nova Scotia, the coast of Maine, and around Cape Cod. Distribution of 28 larvae taken with plankton recorders during *T. N. Gill* cruises was similar to that for the 1-metre net hauls.

LENGTH COMPOSITION

Size compositions of larvae by months are given in Table II, and Fig. 6 and 7. For Fig. 6, an arbitrary division of the larvae into small (4–9 mm.), medium (10–19 mm.) and large (20–50 mm.) size groups has been made.

In September 1956, 69.1% of the larvae taken were in the small, 30.3% in the medium, and 0.6% in the large size-categories. In September 1957, 96.0% of the larvae were small and the remaining 4.0% of medium size. In October 1956, there

TABLE II. Length frequencies of herring larvae taken in the Bay of Fundy and Gulf of Maine.

	1956				1957						1958	
Length	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
mm.	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*
4	0	...	...	...	...	...	5	2	...	...	...	...
5	14	5	...	...	...	...	29	56	...	...	...	...
6	64	48	...	...	...	...	53	96	...	2	...	...
7	41	86	...	...	...	...	64	144	4	1	...	...
8	43	99	...	...	...	...	29	100	89	1	...	...
9	59	71	...	...	...	...	9	69	32	0	...	...
10	44	37	5	...	...	...	1	48	3	2	...	...
11	15	27	8	...	...	...	1	35	2	6	...	...
12	11	23	18	...	...	...	1	98	14	5	...	...
13	6	17	20	2	...	...	0	126	18	12	...	...
14	3	19	22	10	...	...	0	155	8	12	...	...
15	11	16	28	42	...	...	1	181	13	12	2	...
16	2	15	32	102	...	...	2	86	23	12	2	...
17	1	9	32	197	...	...	0	38	29	12	1	...
18	2	5	35	326	...	...	1	34	30	9	0	...
19	2	5	26	396	...	...	1	22	25	16	0	...
20	0	1	18	421	...	...	...	25	12	16	0	...
21	2	7	24	428	...	...	...	25	13	17	4	1
22	...	3	21	391	1	1	...	23	16	13	4	0
23	...	4	17	173	1	1	...	14	4	13	3	3
24	...	5	22	110	2	0	...	8	4	18	4	2
25	...	9	29	78	2	0	...	12	3	14	4	2
26	...	2	25	70	3	0	...	8	1	12	3	4
27	...	0	31	95	4	5	...	7	0	8	6	2
28	...	1	29	93	7	5	...	4	1	7	4	3
29	...	...	21	129	9	5	...	7	0	8	6	5
30	...	...	18	125	9	4	...	8	1	8	10	5
31	...	...	8	49	8	2	...	3	...	6	10	2
32	...	...	8	26	10	3	...	5	...	3	7	3
33	...	...	5	11	9	6	...	0	...	3	5	2
34	...	...	7	7	9	7	...	1	...	3	4	1
35	...	...	3	4	9	7	...	1	...	1	4	1
36	...	...	0	2	11	8	...	1	...	0	4	3
37	...	...	0	0	14	9	...	0	...	1	1	0
38	...	...	0	1	14	13	...	0	...	1	1	1
39	...	...	0	...	14	16	...	0	...	...	2	2
40	...	...	1	...	20	19	...	1	...	...	...	1
41	...	...	1	...	15	20	...	...	...	...	...	1
42	...	...	1	...	7	24	...	...	...	...	...	0
43	...	...	...	...	1	23	...	...	...	...	...	0
44	...	...	...	...	1	16	...	...	...	...	...	0
45	...	...	...	...	0	14	...	...	...	...	...	0
46	...	...	...	...	1	3	...	...	...	...	...	0
47	...	...	...	...	0	2	...	...	...	...	...	0
48	...	...	...	...	1	1	..	...	...	...	...	1
49	...	...	...	...	1	...	...	...	...	...	...	0
50	...	...	...	...	...	...	...	...	...	...	...	1
Totals	320	514	515	3,198	183	214	197	1,443	345	254	91	46

were still large numbers of small larvae (60.1%) but in October 1957, the numbers of small larvae had fallen off considerably from the previous month and represented 32.2% of the total catch. The majority of the larvae (57.0%) taken in October 1957 were in the medium size group. No small herring larvae were taken after October in 1956 but in 1957, 32.2% of the November catches and 1.6% of the December catches were small. This tends to confirm a later spawning on

Georges Bank in 1957 than in the previous year. For both seasons January and February samples contained no newly hatched larvae but for these months in 1958 there were more of the medium size group than during the same period in 1957.

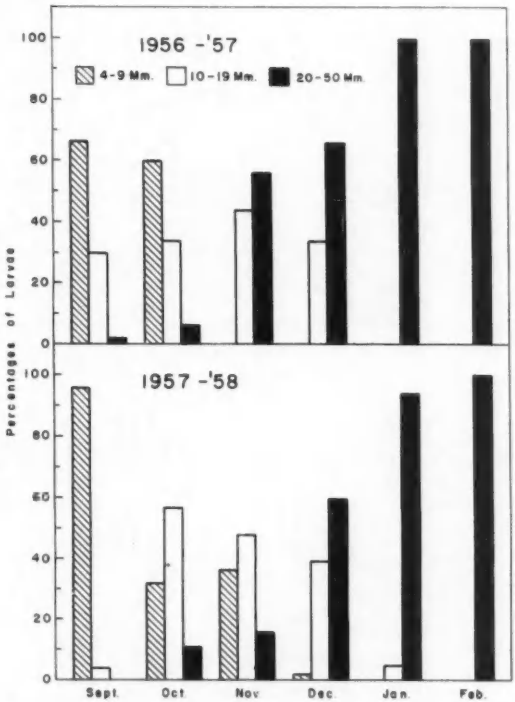

FIG. 6. Variations in the relative abundance of small, medium and large herring larvae during the autumn and winter months.

Length frequency distributions for the two seasons (Table II, Fig. 7) show bi-modality particularly for November and December 1956 and for February, October, and December 1957. The general pattern of larval growth is seen in the shift of histograms to the right as the seasons progress (Fig. 7). In September samples, the range of larval lengths is quite small, and the population appears to be homogeneous (Table II). As the season advances, larvae from other spawnings are added to existing populations, and the size range increases. This may be due to a mixture of larvae from separate populations, but is more likely the result of separate spawnings that occur progressively later within the same parent population.

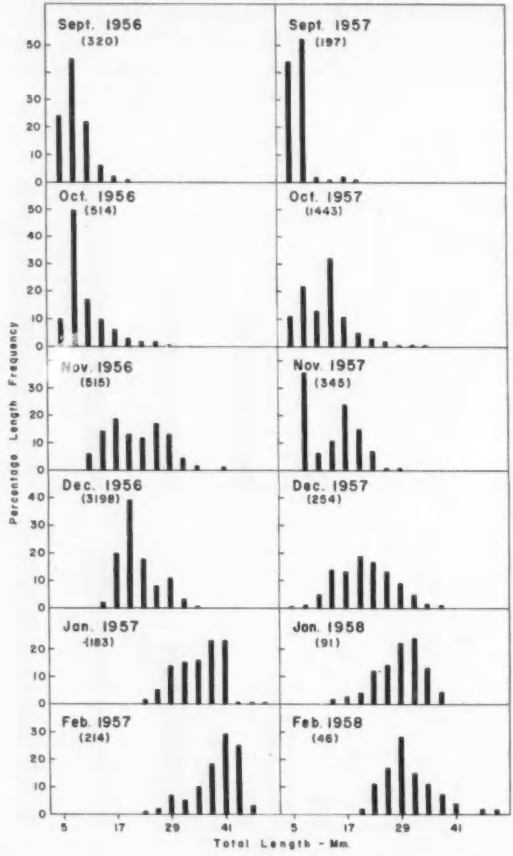

FIG. 7. Length frequency distributions of herring larvae September to February 1956–57 and 1957–58. Data are combined in 3 mm. size groups.

RATE OF GROWTH

An approximate measure of growth can be obtained by plotting mean lengths of larvae taken during each month (Fig. 8). Bowers (1952) presented a growth curve for autumn-spawned herring larvae on the Manx coast off northwestern England. In this area, hatching takes place in October and November. By November surface water temperatures have decreased to about 10°C. from 15°C. in August. Bowers' growth curve was drawn from modal rather than mean lengths.

On Georges Bank, where the majority of larvae were taken, mean monthly surface temperatures varied from 14.1°C. in September 1956, to 9.8°C. in December 1957 (Table III). November temperatures averaged 11.9°C. or nearly 2°C.

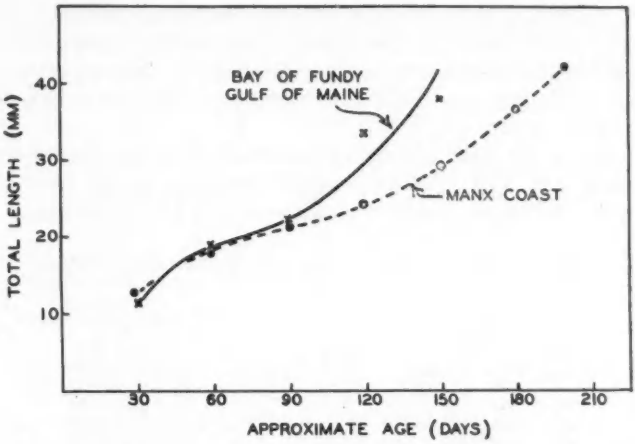

FIG. 8. Growth rates of herring larvae (data for Manx coast from Bowers, 1952).

TABLE III. Mean water temperatures (degrees Centigrade) recorded by bathythermograph on Georges Bank. Numbers of monthly observations are in parentheses.

	1956				1957		1958
Depth	Sept. (28)	Oct. (25)	Nov. (29)	Dec. (7)	Jan. (23)	Dec. (21)	Jan. (21)
feet	°C.	°C.	°C.	°C.	°C.	°C.	°C.
Surface	14.1	13.9	11.9	10.7	5.7	9.8	7.9
30	13.0	13.8	11.8	10.7	5.7	9.7	7.9
50	12.9	13.7	11.8	10.7	5.7	9.7	7.9
100	12.4	13.6	11.9	10.7	5.7	9.8	7.9
150	13.1	13.3	10.8	...	5.7	9.9	8.1

higher than off the Manx coast. Hatching on Georges Bank takes place from September to November in some seasons.

Figure 8 shows a striking similarity between growth curves for the Bay of Fundy–Gulf of Maine and the Manx areas for the first 3 months (90 days). Subsequently, growth rate is more rapid in the Bay of Funday–Gulf of Maine area than on the Manx coast. This may be accounted for by higher surface water temperatures on Georges Bank. Supporting evidence for substantial growth in January and February (estimated 120 and 150 days after hatching) is available from studies of the scales of 1- and 2-year-old herring from the Bay of Fundy and the Gulf of Maine areas. Examinations of scales show that new annual growth zones on the scales of "sardine" herring are apparent in January (unpublished data).

DAY AND NIGHT CATCHES OF HERRING LARVAE

Day and night catches for the September to February cruises are given in Table IV. Division between day and night was made on a 12-hour basis with the dividing points at 6 a.m. and 6 p.m. There were 930 tows taken, 493 during the day and 437 at night.

Total catches for both seasons show that 27.2% of the larvae were taken during the day and 72.8% during the night. Calculated on the basis of average catch per tow, 24.9% were caught during the day and 75.1% at night.

TABLE IV. Day and night catches of herring larvae, by months.

Period	Day		Night		Total
	no.	%	*no.*	%	*no.*
Sept. 1956	4,555	81.0	1,064	19.0	5,619
Oct. 1956	5,909	91.6	544	8.4	6,453
Nov. 1956	25	1.5	1,610	98.5	1,635
Dec. 1956	2,245	12.3	16,074	87.7	18,319
Jan. 1957	1	0.5	195	99.5	196
Feb. 1957	18	6.3	241	93.7	259
Total	12,753	39.3	19,728	60.7	32,481
Sept. 1957	72	1.7	4,115	98.3	4,187
Oct. 1957	570	4.7	11,447	95.3	12,017
Nov. 1957	23	6.6	324	93.4	347
Dec. 1957	60	22.1	211	77.9	271
Jan. 1958	4	4.3	89	95.7	93
Feb. 1958	7	15.2	39	84.8	46
Total	736	4.3	16,225	95.7	16,961
Grand total	13,489	27.2	35,953	72.8	49,442

Catches were made chiefly at night except on September 25 and on October 22 when 4,522 and 5,726 larvae respectively were taken in the late afternoon.

Differences between day and night catches were particularly evident in January and February collections when from 84.8 to 99.5% of the larvae were caught at night. During these months 529 of the 534 larvae caught were more than 19 mm. long (mean lengths 33.2 to 37.6 mm.). At these sizes larvae may be expected to avoid a plankton net particularly during daylight hours.

These results are in agreement with those of Bridger (1956) who found a similar relationship between day and night catches of herring larvae.

SPAWNING AREAS AND SEASONS

From sizes and abundance of larvae taken, spawning areas have been determined (Fig. 9). Jean (1956) reported larvae as small as 4 mm. in the Gulf of St. Lawrence. In northern Scotland, herring larvae hatch at 6 to 8 mm. (Fage, 1920). Bower (1952) reported that newly hatched larvae in Manx waters vary from 6 to 9 mm. in length.

In determining the spawning grounds in the Gulf of Maine and the Bay of Fundy, larvae from 4 to 9 mm. in total length were considered newly hatched

and not far removed from the spawning areas. In a few instances, chiefly in southwest Nova Scotia, direct evidence of spawning is available from collections of eggs but, in general, newly hatched larvae have been used as indicators of spawning grounds.

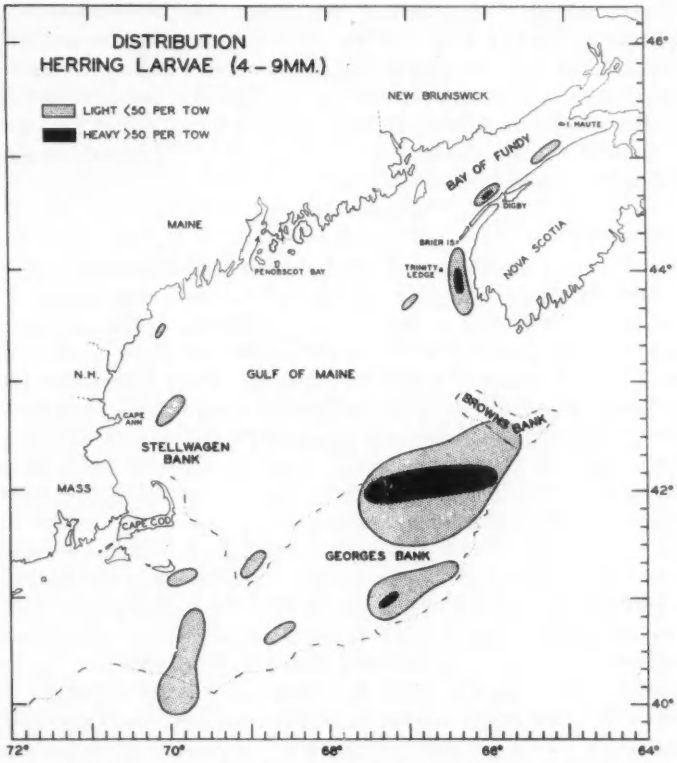

FIG. 9. Herring spawning areas in the Bay of Fundy and the Gulf of Maine estimated from the distribution of newly hatched (4-9 mm.) larvae.

AREAS

The largest spawning area in the Gulf of Maine is on the northern edge of Georges Bank (Fig. 9). This is a shoal area, varying in depth from 3½ fathoms to 50 fathoms. It is characterized by strong tidal currents and heavy mixing. The bottom varies from a granular boulder type to a fine sandy type (Wigley, 1956). Newly hatched herring larvae were found in vary large numbers in this area and as many as 5,726 have been taken in a single, 15-minute plankton tow.

Fig. 9 also shows that herring spawn in the Bay of Fundy from the Seal Island group northward along the Nova Scotia coast to Digby. Another spawning area lies just north of Digby and could, presumably, be an extension of the

first area. Depths vary from 3 to 50 fathoms. Temperatures are fairly uniform from top to bottom due to strong tidal mixing. Character of the bottom has not been described.

Other spawning areas are not very extensive, but may contribute to the stocks of herring in the region. Although very few larvae were taken, there is evidence of small spawnings around Penobscot Bay, Stellwagen Bank, and Nantucket shoals. Moore (1898), Huntsman (1919) and Bigelow and Schroeder (1953) reported an important spawning in the waters south of Grand Manan. Leim (1958) reported the presence of recently hatched larvae in the southern Grand Manan area seasonally from 1917 to 1955. It is evident that spawnings occur regularly in this area but not to the same extent as in southwestern Nova Scotia and on Georges Bank.

Spring Spawning

McNairn (1933) reported small spring spawnings at the heads of the Bay of Fundy and St. Mary Bay. Fish and Johnson (1937) also reported spring spawnings in the Fundy region. Bigelow and Schroeder (1953) reported a few instances of spring spawning in the inshore waters of Nova Scotia and New Brunswick. Mr. E. G. Sollows (personal communication) found some larvae in May near Tucket Island and in St. Mary Bay that were almost certainly spawned in the spring. Mr. John B. Colton, Jr. (unpublished data) caught a few small larvae (9–10 mm.) on Georges Bank and along the coast of Maine during the spring of 1955 and 1956. Six spring-spawned larvae were taken in the Passamaquoddy region in *Prince* tows (unpublished data).

There were few instances of spring-spawned larvae being taken during the course of this investigation. In March 1958, a cruise covering the Grand Manan area, the entrance to the Bay of Fundy and St. Mary Bay showed no newly hatched larvae. A few of the large larvae caught in September and October 1956 and 1957 may have been spawned in late spring or early summer.

It is evident that, for the Gulf of Maine and the Bay of Fundy region, spring spawning is very light and very much less in importance than the heavy autumn spawning. Graham (1936) also found that "spring spawning produced no considerable contributions to the herring stock [in the Bay of Fundy area]."

Autumn Spawning

Most Fundy herring spawn in summer or autumn (McNairn, 1933). Fish and Johnson (1937) found that herring spawn in the Gulf of Maine in summer and autumn but in the Fundy region both spring and autumn spawning takes place. Bigelow and Schroeder (1953) reported heavy spawnings southwest of Grand Manan, around the Trinity Ledges off southwestern Nova Scotia, and light irregular spawnings along the Maine coast.

Heavy spawnings occurred on Georges Bank and along southwestern Nova Scotia from August to October in 1956 and 1957. There was no evidence of spawning in November and December of 1956, but there were signs of a light spawning in November and December, 1957. Whiting fishermen report that

"mature herring arrive on Georges Bank in August and hang just off the northern edge until conditions are right, then, moving into the shoal areas, they spawn."

It is possible to establish a general pattern of movements of herring larvae from spawning grounds on the basis of known non-tidal surface currents. Day (1957) found that current patterns on Georges Bank shift with seasons and prevailing winds. Assuming that currents are important means of distributing larvae, we can speculate on their movements. On the basis of Day's current patterns the larvae spawned on the northern edge of Georges Bank would be swept across Browns Bank towards the southern coast of Nova Scotia. Larvae found elsewhere on Georges Bank would be swept southward. Nantucket shoals larvae would appear along Rhode Island and New Jersey while Stellwagen larvae would be swept southward along Cape Cod. In the Bay of Fundy, movement is somewhat more complex, but would be northward along the southwest coast of Nova Scotia and southward along the coast of New Brunswick and Maine. Eddies complicate this movement, but in general, it will be counter-clockwise.

SUMMARY AND CONCLUSIONS

1. Investigations to discover the breeding grounds, the nursery areas, the survival, growth and methods of transport of the larvae of herring that populate the Passamaquoddy region of New Brunswick and Maine were initiated jointly in 1956 by the Fisheries Research Board of Canada and the U.S. Fish and Wildlife Service.

2. Offshore cruises with plankton nets and Hardy continuous plankton recorders were carried out in the Bay of Fundy and Gulf of Maine from September through February in 1956–57 and 1957–58.

3. During the two seasons, 49,442 larvae were taken in 1-metre net hauls and 212 in recorders. In addition, 30 larvae were available for study from *Prince* station tows and 353 from *T. N. Gill* cruises.

4. Largest numbers of larvae were taken in September and October of each year. Catches decreased sharply in November and were very small in January and February.

5. Larvae were abundant only in the Bay of Fundy and on Georges Bank. Small numbers were taken occasionally throughout most of the survey area.

6. Newly hatched larvae (4 to 9 mm.) were found chiefly in September and October. In some seasons hatching may extend well into November and possibly into December. Growth is slow and larvae, presumably from September and October hatchings, are found in February.

7. Growth in the Bay of Fundy-Gulf of Maine area is faster than for the Manx area in the Irish Sea.

8. About 73% of all larvae in plankton nets were taken at night. The difference between day and night catches was more pronounced for large larvae (20 to 50 mm.).

9. The largest spawning area in the Gulf of Maine is on the northern edge of Georges Bank. Large spawnings occur off the Nova Scotia coast from Trinity

Ledges to Digby. Small spawnings occur in Penobscot Bay, on Stellwagen Bank, Nantucket shoals and south of Grand Manan.

10. Late summer and autumn spawnings are undoubtedly the major contributors to the herring stocks in the Bay of Fundy and Gulf of Maine. Spring spawnings are of only minor importance.

11. Larvae are found in the upper water layers and are probably carried from the spawning grounds by the non-tidal surface currents. Surface current patterns suggest that some larvae from Georges Bank spawnings are carried northward to Nova Scotia coast but the majority of them may be carried southward.

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3: 429 (heat budget of sea in vicinity)
Trites, Ronald Wilmot
1: 79 (surface water circulation over Scotian Shelf)
6: 1247 (water layers in Laurentian Channel)
Trout, brook (*Salvelinus fontinalis*)
4: 607 (preferred temperature)
6: 1145 (review of investigations)
6: 1403 (movements in fresh and salt water)
Trout, cutthroat (*Salmo clarki*)
1: 27 (competition and mortality)
5: 791 (early investigations)
Trout, hybrid
4: 607 (preferred temperature and vertical distribution in nature)
Trout, Kamloops (*Salmo gairdneri*)
4: 573 (effect of exercise on blood)
Trout, lake (*Cristivomer namaycush*)
4: 749 (vital statistics for L. Opeongo, Ont.)
Trout, rainbow (*Salmo gairdneri*)
4: 559 (toxicity of cyanide and detergents to)
5: 791 (early investigations)
Turbidity
6: 1403 (in relation to trout movements)

U

Ungava Bay
2: 155 (physical oceanography)
2: 219 (bearded seal)

V

Vancouver Island, B.C.
5: 1103 (chum and pink salmon production)
Vertebrae
3: 275 (number in capelin)
Vision, of zooplankton and fishes
3: 464 (stimulation by light)
Vessels, research
5: 766 (*A. P. Knight*)
5: 770 (*Investigator No. I*)
5: 773 (*Alta*)
6: 1129 (*Sea Gull*)
6: 1132 (*Edward E. Prince*)
6: 1137 (*Zoarces*)
6: 1146 (*J. J. Cowie*)
6: 1149, 1453 (*Harengus*)
6: 1453 (*Silver Bay*)
Virtual population method
4: 749 (modification of procedure)
Vladykov, Vadim Dmitrovich
1: 47 (*Lampetra ayresii*)
Volunteer investigators
5: 782 (at Nanaimo)
6: 1156 (and others, at St. Andrews)

W

Waldichuk, Michael
5: 1065 (drift bottle observations in Strait of Georgia)
Walleye, yellow (*Stizostedion vitreum*)
2: 203 (in Heming L., Manitoba)
4: 607 (preferred temperature and vertical distribution)
Wapun Lake, Manitoba
2: 203 (limnology)

Water level
5: 1103 (in relation to salmon spawning success)
6: 1403 (in relation to trout movements)
Watson, Nelson Herbert Frank
2: 203 (limnology of Heming L., Man.)
Whale, white (*Delphinapterus leucas*)
1: 1
White, Harley Clifford
6: 1143
Whitefish (*Coregonus clupeaformis*)
2: 203 (Heming L., Manitoba)
Whiting (*Merluccius bilinearis*)
4: 625 (distribution and landings, in relation to temperature and fishery)
Wickett, William Percy
2: 229 (salmon egg development with low oxygen)
5: 797 (carbon dioxide and salmon eggs)
5: 1103 (environmental effects on salmon production)
Wilder, Donald George
6: 1345 (catchability of lobsters)
Wind effects
1: 78 (on surface waters of Scotian Shelf)
5: 1097 (on drift bottles)
6: 1170 (on sea level)
6: 1178 (in discoloration of Arctic ice)
Withler, Frederick Curtis
5: 1007 (sockeye spawning and production)
Wood borers (*see also* Shipworm)
6: 1152 (review of investigations on)

Y

Yield (*see also* Statistics)
5: 831 (in relation to minimum size of lingcod)
5: 991 (computation from numerical models)
5: 1007 (of Skeena sockeye)

Z

Zooplankton (*see also* Plankton)
3: 464 (vision and stimulation by light)
6: 1186 (Foraminifera in Foxe Basin mud and ice)